K.V. SÝKORA

THE LOLIO-POTENTILLION ANSERINAE TÜXEN 1947

in the northern part of the Atlantic domain

THE LOLIO-POTENTILLION ANSERINAE R.TÜXEN 1947 IN THE NORTHERN PART OF THE ATLANTIC DOMAIN

Promotores: Prof. Dr. V.Westhoff
Prof. Dr. M.J.A.Werger

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Dankwoord

Graag wil ik iedereen, die heeft bijgedragen aan het tot stand komen van dit proefschrift, bedanken.

The highest good is like water.
Water gives life to the ten thousand things
and does not strive.
It flows in places men reject and so is like Tao.

Lao Tsu, 6th century B.C.

Aan Conny, Jacinthe en Vera Mei.

Ik zou U gaarne rukken uit het gewoone gebrek, ik meen uit de doemwaardige onaandoenlykheid en onoplettendheid omtrent de Werken van God, welke zo algemeen en zo ongelukkig de Menschen heeft bevangen.

Daarin toch smaakt men die zagte aandoeningen, die met de oorsprongelyke zagtmoedigheid onzer nu verbasterde natuur meest overeenstemmen. Als wy in het gewoel der groote waereld zyn, drukken ons eene menigte van wilde neigingen, die ons gevoelloos maaken voor regte vergenoegingen.

De schoonheid en de volmaaktheid van des Scheppers Werken zyn zodanig groot, dat wy een streelend vermaak vinden, zelfs in de beschouwing van Boomen, van Weiden en van Wildernissen, waarin men anders waanen zou, dat hetzelve niet te vinden zou zyn. Een arme kan zo wel als een ryke, een ongeleerde zo wel als een geleerde, een gemeen zo wel als een groot Man deeze genoeglykheden verkrygen. Alles hangt af van de oplettendheid. De Waereld staat voor allen ter beschouwinge open.

uit:"Katechismus der Natuur" van J.F.Martinet, 1778.

met dank aan Rob Leopold

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Samenvatting

1. Inleiding

Nadat door Westhoff et al. in 1942 c.q. in 1946 een eerste overzicht van de plantengemeenschappen van Nederland werd gepubliceerd, nam de kennis van de Nederlandse vegetatie snel toe. Westhoff gaf in 1979 een historisch overzicht van deze ontwikkeling. In 1969 (Westhoff & Den Held 1969; nagenoeg ongewijzigde herdruk:1975) werd de toenmalige kennis omtrent de samenstelling, synoecologie, syntaxonomie en verbreiding van de Nederlandse plantengemeenschappen voor de laatste maal weergegeven. Uit dit werk blijkt waaruit de toen nog aanwezige hiaten in onze desbetreffende kennis bestonden. Het meest opvallend was wel de geringe kennis die men niet alleen in Nederland, maar ook in de omringende landen had van het verbond, dat toen nog *Agropyro-Rumicion crispi* genoemd werd. Dit proefschrift heeft tot doel, deze leemte op te vullen.

2. Het Zilverschoonverbond (*Lolio-Potentillion anserinae* R.TÜxen 1947).

Dit proefschrift behandelt de syntaxonomie en de synoecologie van het Zilverschoonverbond (*Lolio-Potentillion anserinae* R.TÜxen 1947) in het noordelijke deel van het Atlantische Domein. Op grond van het grote verschil in floristische samenstelling en in standplaats splitste ik in 1980 (publikatie 1, dit proefschrift) de gemeenschappen van langdurig overstroomde weilanden (*Lolio-Potentillion anserinae* R.TÜxen 1947) af van de Zandhavergemeenschappen die voorkomen op grote wierhopen langs de kusten van Noord-Europa (*Agropyro-Rumicion crispi* Nordhagen 1940) en die thans gerekend dienen te worden tot de klasse *Elymetea arenarii* TÜxen 1966. Beide vegetatietypen waren voordien verenigd in het *Agropyro-Rumicion crispi* Nordhagen 1940 em. R.TÜxen 1950.

Het Zilverschoonverbond behoort tot de Weegbreeklasse (*Plantaginetea majoris*) en de Fioringrasorde (*Agrostietalia stoloniferae*). Een fytocoenose kan tot dit verbond worden gerekend, wanneer de daarin optredende, hieronder te noemen kensoorten, benevens de constante begeleider *Poa trivialis* er samen meer in voorkomen (technisch gesproken: een

groter groepsaandeel hebben) dan de gezamenlijke kentaxa van enig ander fytocoenon. Dit is overeenkomstig de formulering op pagina 31 van Westhoff & Den Held (1969).Kensoorten van het Zilverschoonverbond zijn: Fioringras (*Agrostis stolonifera*), Geknikte vossestaart (*Alopecurus geniculatus*), Krulzuring (*Rumex crispus*), Zeegroene Rus (*Juncus inflexus*); constante begeleider is Ruw beemdgras (*Poa trivialis*). Verder kunnen er de volgende kensoorten van de Weegbreeklasse (*Plantaginetea majoris*) in voorkomen: Zilverschoon (*Potentilla anserina*), Grote weegbree (*Plantago major*), Engels raaigras (*Lolium perenne*) en Straatgras (*Poa annua*). Het voorstel van TÜxen (1970) om de *Plantaginetalia majoris* met inbegrip van het *Lolio-Potentillion* tot de *Molinio-Arrhenatheretea* (klasse der vochtige graslanden) te rekenen, werd door mij in dit proefschrift niet overgenomen. De floristische samenstelling van deze gemeenschappen verschilt aanzienlijk van die van de *Molinio-Arrhenatheretea* (publikatie 2). Op grond van de in het Atlantisch Domein verzamelde gegevens is er geen aanleiding, over te gaan tot een splitsing van het *Lolio-Potentillion* in de drie verbonden *Eu-Agropyro-Rumicion*, *Loto-Trifolion* en *Juncion effusi*, zoals in 1963 door Doing werd voorgesteld. Doing kwam hiertoe op grond van een in 1961 gehouden, maar pas in 1966 gepubliceerde voordracht van Westhoff en van Leeuwen, die echter niet verder waren gegaan dan de eventuele opstelling van de verbonden *Loto-Trifolion* en *Juncion effusi* als een mogelijkheid te opperen. Nadien (Westhoff et al. 1962) gingen zij ertoe over, het *Loto-Trifolion* als onderverbond van het *Agropyro-Rumicion crispi* te beschouwen. In aansluiting daarop achtten Westhoff en Den Held (1969) de indeling van Doing (1963) nog voorbarig; de uit de opvatting van Doing (l.c.) voortvloeiende verheffing van het verbond *Agropyro-Rumicion crispi* (in de tot dan toe gebruikte zin) tot een orde *Festucetalia arundinaceae* wezen zij af.

De in het Zilverschoonverbond voorkomende soorten bestaan voornamelijk uit " kruipende " hemicryptofyten en rhizoomgeofyten, dat wil zeggen uit planten met lange boven- of ondergrondse uitlopers. Zij kunnen zich hierdoor snel vegetatief uitbreiden en zo de in het vegetatiedek ontstane gaten dichten.

Het Zilverschoonverbond komt voor in uiterwaarden, langs oude rivierlopen (strangen), doorbraakkolken (wielen), laagten met stagnerend

water, langs drinkpoelen voor het vee, langs sloten en in greppels, op hoger gelegen kwelders en langs oude kreken. Het is te vinden op uiteenlopende, relatief voedselrijke, hydromorfe bodems, variërend van zand tot zware klei en van minerale tot venige bodems. De meeste van de voor dit verbond kenmerkende soorten komen optimaal voor op matig stikstofrijke tot stikstofrijke bodems met een tamelijk snelle mineralisatie. De voornaamste factoren voor het ontstaan of de instandhouding van het Zilverschoonverbond zijn verder overstroming van het grasland gedurende winter en lente, en begrazing.

De voor dit verbond kenmerkende soorten behoren tot de trichohygrofyten sensu Hejny 1960, dat wil zeggen dat kieming en ontwikkeling plaats vinden in de terrestrische oecofase wanneer de bovenste bodemlagen nog tamelijk vochtig zijn. In deze fase vinden ook bloei en rijping van de zaden plaats. Bij een lage temperatuur van het water kunnen deze planten overstroming gedurende langere tijd (winter en voorjaar) overleven. Bovendien verdragen deze soorten een secundaire overstroming in het groeiseizoen. Overstroming kan de ademhaling ernstig bemoeilijken en leidt bovendien tot de vorming van giftige stoffen in de bodem, zoals Mn^{2+}, Fe^{2+}, sulfiden, CO_2, organische zuren en methaan. Bij de soorten die overstroming verdragen zijn hieraan verschillende aanpassingen aangetroffen, bijvoorbeeld het voorkomen van zuurstofdiffusie door stengel, rhizoom en wortel en de mogelijkheid om bij zuurstofgebrek over te schakelen op een andere stofwisselingsweg, waarbij in plaats van het giftige ethanol uitsluitend niet-giftige stoffen zoals appelzuur (malaat) als voorlopig eindprodukt worden opgeslagen. Overstromingsgevoelige soorten vormen onder deze omstandigheden het giftige ethanol en kunnen hierdoor afsterven (voor literatuurreferenties zie publikatie 2).

Onder invloed van de beweiding ontstaan in de zachte, natte bodem vaak diepe hoefafdrukken. Deze betreding is echter niet noodzakelijk voor de ontwikkeling van het Zilverschoonverbond. Onbetreden maar toch goed ontwikkeld *Lolio-Potentillion* komt vaak voor op net buiten een hek gelegen plaatsen, die nog binnen reikwijdte van het vee liggen. Het is zeer aannemelijk dat het Zilverschoonverbond al in prehistorische tijden voorkwam, aangezien destijds de rivieren, die nog niet door de mens waren bedwongen, veelvuldig buiten hun oevers traden en

er bovendien grote herbivoren voorkwamen.

Het is naar mijn mening weinig zinvol om het Zilverschoonverbond een storingsgemeenschap te noemen zoals wel gedaan wordt. De fluctuatie in de waterstand is voor deze gemeenschap geen storing maar een noodzaak. Juist het wegvallen van deze natuurlijke schommelingen zou voor het Zilverschoonverbond een ernstige storing betekenen. De voornaamste factoren die de differentiatie binnen het verbond teweeg brengen, zijn de waterhuishouding in de zomer, het zoutgehalte en de trofiegraad (voedselniveau) van de bodem.

Als gevolg van een ernstige toename van de menselijke invloed gaat tegenwoordig deze voor het Noordwesteuropese laagland zo kenmerkende gemeenschap sterk achteruit. Dit is voornamelijk het gevolg van ontwatering en het op grote schaal gebruiken van anorganische meststoffen en herbiciden. Daarnaast vormen op de ene plaats de overmatige begrazing, elders het uit beweiding nemen van nat grasland een ernstige bedreiging. In 1969 (Westhoff & Den Held) had men nog de indruk, dat van het *Agropyro-Rumicion crispi* als synanthroop half-natuurlijk oecosysteem, verwacht mocht worden, dat het , als gevolg van de toenemende " druk op het milieu " (dat wil zeggen toenemende anthropogeen toegevoegde dynamiek) in oppervlakte en wellicht ook in verscheidenheid zou toenemen. Het tegendeel is echter het geval geweest, en wel doordat de vernietiging van onze half-natuurlijke landschappen een omvang en draagwijdte heeft gekregen die destijds nog niet konden worden voorzien. De achteruitgang is vanuit het oogpunt van natuurbeheer des te meer te betreuren, omdat dergelijke natte graslanden van groot ornithologisch belang zijn. Zij bieden nestelgelegenheid aan steltlopers en andere, op de grond broedende, soorten en vormen tevens belangrijke fourageergebieden (Owen & Cadbury 1975, Owen & Thomas 1979, Thomas 1980). Zo voeden Zwaan en Smient zich bijvoorbeeld met Geknikte vossestaart (*Alopecurus geniculatus*), Fioringras (*Agrostis stolonifera*) en Mannagras (*Glyceria fluitans*). Andere eendachtigen consumeren de zaden van Kruipende boterbloem (*Ranunculus repens*), Moerasvergeet-mij-nietje (*Myosotis scorpioides*), van *Cyperaceae* als Waterbies (*Eleocharis palustris*) en van *Polygonaceae* als Krulzuring (*Rumex crispus*), Kluwenzuring (*R.conglomeratus*) en Veenwortel (*Polygonum amphibium*).

3. De inwendige verscheidenheid

Aan de hand van de syntaxonomische tabellen zijn vier associaties, elf subassociaties, een derivaatgemeenschap en een basisgemeenschap onderscheiden. De beide laatste konden worden onderverdeeld in een aantal typen. Aan het einde van deze samenvatting volgt een determinatiesleutel van alle besproken gemeenschappen. Bovendien wordt van iedere subassociatie een type-opname gegeven, omdat dit elders nog niet is gebeurd.

De volgende gemeenschappen zijn in dit proefschrift behandeld (publikaties 2,3 en 4):

Klasse: *Plantaginetea majoris* R.Tüxen & Preising 1950
Orde: *Agrostietalia stoloniferae* Oberdorfer, Müller & Görs 1967
Verbond: *Lolio-Potentillion anserinae* R.Tüxen 1947

Ranunculo-Alopecuretum geniculati Tüxen 1937 (180 opnamen)
subassociatie: *typicum* Sýkora 1982
roripetosum sylvestris Sýkora 1982
equisetetosum palustris Sýkora 1982

Nasturtio-Alopecuretum geniculati Sýkora 1982 (66 opnamen)
subassociatie: *ranunculetosum scelerati* Sýkora 1982
stellarietosum alsinis Sýkora 1982

Triglochino-Agrostietum stoloniferae Konczak 1968(104 opn.)
subassociatie: *ranunculetosum repentis* Sýkora 1982
juncetosum gerardii Sýkora 1982
inops Sýkora 1982

derivaatgemeenschap van *Festuca arundinacea-* [*Lolio-Potentillion*] (21 opnamen)
Lolium perenne-type
Alopecurus geniculatus-type

basisgemeenschap van *Agrostis stolonifera-* [*Lolio-Potentillion*] (125 opnamen)
Trifolium fragiferum-Ranunculus sardous-type
Scirpus maritimus-Juncus bufonius-type
Juncus inflexus-Rumex obtusifolius-type
Eleocharis uniglumis-Carex otrubae-type
Juncus inflexus-Carex otrubae-type
Trifolium fragiferum-Carex hirta-type
Juncus effusus-Bolmus lanatus-type

De associatie van Kruipende boterbloem en Geknikte vossestaart (*Ranunculo-Alopecuretum geniculati*), de "type"-associatie van het Zilverschoonverbond, is beperkt tot standplaatsen met een zeer dynamische waterstand. Dit wil zeggen dat het overstromingswater enkele meters diep kan zijn, terwijl in de zomer het grondwater zo diep wegzakt, dat de bovenste laag van de bodem kan uitdrogen.
Het verschil in floristische samenstelling tussen de drie subassociaties wordt veroorzaakt door een verschillende invloed van het grondwater in het groeiseizoen. De subassociatie *rorippetosum sylvestris* komt voor op standplaatsen met een lage grondwaterstand in de zomer. Het grondwater bevindt zich dan vaak meer dan een meter beneden het maaiveld. Bij de subassociatie *equisetetosum palustris* staat het grondwater nooit ver onder het maaiveld, meestal niet dieper dan 30 cm. De subassociatie *typicum* neemt, wat de waterhuishouding betreft, een tussenpositie in ten opzichte van beide voorgaande subassociaties.

Het *Nasturtio-Alopecuretum geniculati*, het *Triglochino-Agrostietum stoloniferae* en het *Agrostio-Trifolietum fragiferi* werden samen ondergebracht in een associatiegroep, i.c. de associatiegroep met Slanke waterbies (*Eleocharis uniglumis*). Deze associatiegroep, te herkennen aan de kensoorten *Eleocharis uniglumis*, *Carex otrubae* en de differentiërende soort *Phragmites australis*, komt, in tegenstelling tot het *Ranunculo-Alopecuretum* , voor op standplaatsen met een minder dynamische waterhuishouding en een nooit uitdrogend bodemoppervlak.

De associatie van Slanke waterkers en Geknikte vossestaart grenst in het veld vaak aan gemeenschappen van de Waterkers-Vlotgrasorde (*Nasturtio-Glycerietalia*) en van het Moerasandijvieverbond (*Bidention*). Zij komt voor langs sloten, drinkpoelen en oude kreken op zeer zachte, sterk betreden zandige of venige, voedselrijke kleibodems die vrijwel het hele jaar met water verzadigd zijn. Het waterniveau ligt gedurende een groot deel van het jaar 10-20 cm boven het maaiveld.

De subassociatie *stellarietosum alsinis* werd uitsluitend aangetroffen in Ierland en wel op een in vergelijking met de subassociatie *ranunculetosum scelerati* waarschijnlijk minder voedselrijke, matig zure bodem.

In niet kunstmatig bemeste weilanden, op relatief voedselarme en matig zure bodems groeit de associatie van Moeraszoutgras en Fiorin-

gras (*Triglochino-Agrostietum stoloniferae*). Deze gemeenschap vertoont enige floristische verwantschap met het verbond van Zompzegge en Gewone zegge (*Caricion curto-nigrae*), dat wil zeggen met mesotrafente kalkmijdende Kleine zeggengemeenschappen. Zij is zeer gevoelig voor bemesting en wordt daarom bedreigd door de intensivering van de landbouw.

Terwijl de subassociatie *ranunculetosum repentis* op zoete bodem voorkomt, is de subassociatie *juncetosum gerardii* beperkt tot licht brakke standplaatsen, bijvoorbeeld de hoger gelegen delen van kwelders.

De subassociatie *inops* werd aangetroffen op overmatig betreden en overbegraasde plaatsen en onder omstandigheden die te droog zijn voor de beide andere subassociaties.

De associatie van Fioringras en Aardbeiklaver (*Agrostio-Trifolietum fragiferi*) komt uitsluitend voor op brakke bodems. De subassociatie *typicum* werd uitsluitend aangetroffen op licht brakke bodem buiten het bereik van de zee en wel aan de landzijde van de zeedijk, in primaire duinvalleien, in greppels langs een kreek en in een weiland op de bodem van een kleiafgraving. De subassociatie *festucetosum rubrae* wordt tijdens stormvloed met zeewater overspoeld en komt voor op de hoger gelegen delen van de kwelder en in sluftervlakten. De subassociatie *inops* doet zich voor als laag gelegen plekken, omgeven door een dichte vegetatie, gedomineerd door Zeerus (*Juncus maritimus*), Duinriet (*Calamagrostis epigejos*), Knopbies (*Schoenus nigricans*) of Rood zwenkgras (*Festuca rubra*). Deze gemeenschap wordt slechts zeer extensief begraasd door schapen, soms ook door koeien en nu en dan zelfs voornamelijk door konijnen. Ook deze subassociatie wordt door stormvloed overspoeld.

Onder bijzondere omstandigheden kunnen gemeenschappen ontstaan die, omdat ken- en differentiërende soorten ontbreken, niet op associatieniveau te plaatsen zijn, maar die wel duidelijk tot het Zilverschoonverbond behoren. Zo ontstaat onder invloed van onregelmatige beweiding, meestal door paarden, de derivaatgemeenschap van *Festuca arundinacea-[Lolio-Potentillion]* . Hierin heeft Rietzwenkgras (*Festuca arundinacea*) een hoge bedekking. Een derivaatgemeenschap is een fytocoenose bestaande uit ken- en differentiërende soorten van hogere syntaxonomische eenheden, uit begeleidende soorten en uit een dominante soort.
Bij een selectieve lage begrazingsdruk is meer voedsel voorhanden dan nodig is en dit leidt ertoe dat het vee de onsmakelijke soorten als

Festuca arundinacea vermijdt, waardoor deze zich uit kunnen breiden. Van de twee onderscheiden typen groeit het *Lolium perenne*-type op een bodem die in het groeiseizoen droger is dan die waarop het *Alopecurus geniculatus*-type voorkomt.

Ook de basis- of rompgemeenschap van *Agrostis stolonifera-* [*Lolio-Potentillion*] kan niet op grond van floristische kenmerken tot een van de associaties worden gerekend. Een basisgemeenschap kan ontstaan uit een coenologisch verzadigde gemeenschap (een gemeenschap waarin alle daarvoor karakteristieke ken- en differentiërende soorten aanwezig zijn) (bijvoorbeeld een associatie) ten gevolge van een toename in de -meestal anthropogene - dynamiek waardoor sommige soorten verdwijnen. De voornaamste factor voor het ontstaan van de basisgemeenschap van *Agrostis stolonifera* is storing in de vorm van bijvoorbeeld overmatige betreding, overbegrazing, herbicidengebruik, het deponeren van organisch materiaal, recente begrazing in een voordien onbeweid grasland, ontzilting van recente landaanwinning of overbemesting. Afhankelijk van verschillen in standplaats en aard van de verstorende factoren kan een aantal typen worden onderscheiden.

Het *Trifolium fragiferum-Ranunculus sardous*-type komt voor op brakke, voedselrijke bodem onder invloed van intensieve begrazing, herbicidengebruik en/of overbemesting. Het *Scirpus maritimus-Juncus bufonius*-type heeft dezelfde standplaats maar de bovengenoemde storing is intensiever. Het *Juncus inflexus- Rumex obtusifolius*-type indiceert voedselrijke, basische bodem met een tamelijk droog oppervlak in de zomer; het *Juncus effusus-Holcus lanatus*-type komt daarentegen voor op vochtig blijvende, matig zure en matig voedselarme bodem. Het *Juncus inflexus-Carex otrubae*-type en het *Trifolium fragiferum-Carex hirta*-type worden aangetroffen op plaatsen met overmatige betreding. In het laatste geval is bovendien duidelijk sprake van herbicidengebruik.
Het *Eleocharis uniglumis-Carex otrubae*-type tenslotte wordt aangetroffen op doornatte zware klei, onder invloed van onregelmatige beweiding.

4. Syntaxonomie van het *Junco-Menthetum longifoliae* Lohmeyer 1953, het *Junco-Menthetum rotundifoliae* Oberdorfer (1952)1957 en het *Caricetum vulpinae* Nowinski 1927 (publikatie 5).

Omdat de associatie van Zeegroene rus en Hertsmunt (*Junco-Menthetum longifoliae*) en de associatie van Zeegroene rus en Witte munt (*Junco-Menthetum rotundifoliae*) tot het *Agropyro-Rumicion crispi* werden gerekend, zijn beide gemeenschappen bij deze studie betrokken. Hetzelfde geldt voor de Voszegge-associatie (*Caricetum vulpinae*) die door een aantal auteurs eveneens in dit verbond wordt geplaatst. Westhoff & van Leeuwen (1966) vermoeden dat de Voszegge (*Carex vulpina*) een kensoort van het *Agropyro-Rumicion* zou kunnen zijn en Westhoff & Den Held (1969) plaatsten deze associatie dan ook in dit verbond. Andere auteurs rekenden het *Caricetum vulpinae* tot het verbond van de grote zeggen (*Magnocaricion* W.Koch 1926).

Van de bovengenoemde gemeenschappen werden uit de literatuur opnamen verzameld met een zo groot mogelijke spreiding over Europa en deze werden tot fytosociologische tabellen verwerkt. Uit de resultaten blijkt dat Hertsmunt *(Mentha longifolia)* vaker voorkomt in conglomeraten waarin soorten uit de klasse van de vochtige graslanden (*Molinio-Arrhenatheretea*) overheersen, dan in conglomeraten waarin soorten van de Weegbreeklasse (*Plantaginetea*) domineren.

In een van de conglomeraten vormden soorten van de Rietklasse (*Phragmitetea*) het belangrijkste element. De term conglomeraten werd in dit artikel (publikatie 5) geïntroduceerd. Een conglomeraat bestaat uit een mengsel van fragmenten, dat wil zeggen een mengsel van gemeenschappen, die elk voor zich op grond van de afwezigheid van voldoende diagnostische soorten niet tot een associatie kunnen worden gerekend. Aangezien er geen objectief criterium bestaat om de conglomeraten tot een van de bovengenoemde klassen te rekenen en aangezien de floristische samenstelling van de verschillende conglomeraten sterk uiteenloopt, bestaat de associatie *Junco-Menthetum longifoliae* naar mijn mening niet. *Mentha longifolia* is geen kensoort van het Zilverschoonverbond. De soort vertoont wat betreft zijn epharmonie, dat wil zeggen zijn speciale oecologische eisen, veel overeenkomst met de *Filipendulion*- soorten. De conglomeraten hebben dan ook in het algemeen het karakter van een ruigte ("Hochstaudenflur",d.i. een dichte vegetatie van hoog opgaande,overblijvende kruiden met bebladerde stengels (hemicryptofyta scaposa)).Bij extensieve beweiding zijn de *Plantaginetea*-soorten van ondergeschikt belang; bij toenemende begrazing neemt het aandeel van deze soorten toe en

neemt de bedekkingsgraad van *Mentha longifolia* af.

Van het *Junco-Menthetum rotundifoliae* zijn maar weinig gepubliceerde opnamen voorhanden. Omdat deze bovendien geen eigen kenmerkende soortencombinatie opleveren, en bovendien nog een grote gelijkenis bezitten met een van de conglomeraten met *Mentha longifolia*, moet het bestaan van deze associatie vooralsnog worden verworpen.

In het *Caricetum vulpinae* blijken de soorten van het *Magnocaricion* en van de *Phragmitetea* sterk te overheersen, wat de plaatsing in deze syntaxa rechtvaardigt. Omdat het *Lolio-Potentillion* een vervangingsgemeenschap is van het *Magnocaricion*, wordt het *Caricetum vulpinae* onder invloed van begrazing door het *Lolio-Potentillion* vervangen. De in de literatuur beschreven subassociaties blijken slechts van lokale betekenis te zijn, zodat deze op Europese schaal niet onderscheiden kunnen worden. De voornaamste differentiatie uit zich in een geleidelijke toename van de *Molinio-Arrhenatheretea*-, vooral de *Molinietalia*-en van de *Scheuchzerio-Caricetea*-soorten bij een afname van de hydrologische dynamiek. De associatie heeft een noordelijk-continentale verspreiding en komt optimaal voor in oostelijk centraal Europa.

5. De synoecologie van het Zilverschoonverbond

Om de synoecologie, met name de invloed van de schommelingen in de waterhuishouding op het Zilverschoonverbond na te gaan, werd een meerjarig onderzoek opgezet met behulp van permanente transecten. Dit onderzoek vond plaats in een brakke stenosaleutische omgeving (publikatie 6), dat wil zeggen in brakke standplaatsen met een waterstandsschommeling van ten hoogste 60 cm. Daarnaast werden transecten bestudeerd van zoete, eurysaleutische standplaatsen langs de Waal (publikatie 7). Het verschil tussen hoog en laag water is hier groter dan 80-100 cm en bedraagt in de meeste gevallen zelfs meer dan 5 meter. Het doel van dit onderzoek was drieledig en hield in :

1) het nagaan van de verspreiding van de soorten in relatie tot de overstromingsduur;
2) het beschrijven van eventueel aanwezige zonering in de plantengroei en de relatie daarvan met de hydrologie;
3) het nagaan van de reactie van de verschillende soorten op de jaar-

lijkse schommelingen in de waterhuishouding.

Het *Lolio-Potentillion* ontwikkelt zich optimaal op plaatsen die gedurende winter en lente overspoeld worden. De soorten die het verbond kenmerken, komen ook op niet-overspoelde plaatsen voor wanneer de bodem gedurende het grootste deel van het jaar met water verzadigd is. Zij blijken in staat te zijn, een langdurige overstroming tijdens het groeiseizoen te overleven. De meeste soorten verdragen een overstroming van 21 tot 26 weken gedurende de zomerperiode. Alle in de transecten van het stenosaleutische gebied waargenomen soorten werden aan de hand van de verzamelde waterstandsgegevens gerangschikt in volgorde van de maximale overstromingsduur in het groeiseizoen, waarbij zij nog werden aangetroffen. Bij de gegevens van de eurysaleutische standplaatsen werd voor de rangschikking gebruik gemaakt van een ordinatie (reciprocal averaging). Interpretatie van het ordinatiediagram laat zien dat de tweede as correspondeert met het gedrag van de soorten met betrekking tot de overstromingsduur; langs deze as blijken in het algemeen de relatieve inundatiewaarden en de vochtindicatiewaarden van Ellenberg (1979) in één richting toe te nemen.
Invulling van de stikstofindicatiegetallen van Ellenberg laat een geleidelijke toename zien langs de eerste as, waarbij de soorten met de laagste indicatiewaarden voornamelijk voorkomen in de transecten die zich bevinden aan een binnendijks gelegen doorbraakkolk. Deze transecten ondervinden slechts indirect invloed van het rivierwater, en wel wanneer dit bij een hoge waterstand onder de dijk doorkwelt. De soorten die op overmatige nutriëntentoevoer wijzen bevinden zich uitsluitend in de in de uiterwaard voorkomende transecten. In deze laatstgenoemde transecten werden de hoogste gehalten aan totaal fosfor gemeten, terwijl de laagste waarden voorkwamen langs de doorbraakkolk.
De aanwijzing dat de differentiatie langs de eerste as te maken heeft met het nutriëntenniveau van de bodem wordt versterkt door het feit dat de soorten van de Glanshaverorde (*Arrhenatheretalia*)zich aan de ene kant van de as bevinden, terwijl de soorten van de Tandzaadorde (*Bidentetalia*), de Bijvoetklasse (*Artemisietea*), de Ganzevoetklasse (*Chenopodietea*) en de soorten van de Slijkgroenassociatie (*Eleocharitetum soloniensis*) aan de andere kant zijn geplaatst. Laatstgenoemde syntaxa komen in het veld voornamelijk in stikstofrijk (dit is nitraat- of

ammoniakrijk) milieu voor (nitrofytische syntaxa). De *Arrhenathereta-lia* daarentegen komen op relatief voedselarmere bodem voor.

Twee van de transecten uit het stenosaleutische gebied bleken duidelijk gezoneerd. Achtereenvolgens waren te onderscheiden:
1) een niet-overspoelde zone;
2) een middenzone beneden het maximale waterpeil in de winter;
3) een benedenzone die bijna het hele jaar overspoeld is of die een zachte, sterk betreden, met water verzadigde bodem heeft.
De middenzone kan verdeeld zijn in twee subzones wanneer er een scherp contrast bestaat tussen de overstromingsduur van de bovenste en onderste kwadraten van de middenzone.

In de overige transecten verloopt de verandering in vegetatie geleidelijk. In de transecten van de stenosaleutische standplaatsen is dit te verklaren doordat de bodem van de bovenste kwadraten gedurende een groot deel van het jaar met water verzadigd is, zonder dat er sprake is van overstroming. Deze verzadiging is het gevolg van een hoge grondwaterstand, veroorzaakt door de aanwezigheid van een moeilijk doorlatende kleibodem of van een veenlaag in de ondergrond.
In het eurysaleutische gebied is de afwezigheid van een duidelijke zonering waarschijnlijk het gevolg van de grote onregelmatigheid in het optreden van de overstromingen en de daarmee samenhangende onvoorspelbaarheid van frequentie, duur en diepte ervan.

Een groot aantal soorten vertoonde onder invloed van de hydrologische verschillen tussen de jaren schommelingen in de totale bedekking binnen het transect. Deze ecotopische fluctuaties, dat wil zeggen schommelingen die het gevolg zijn van veranderingen in het ecotoop (klimaat, bodem, waterhuishouding) hadden in de twee onderzochte standplaatstypen een verschillend karakter. In het stenosaleutische milieu had de zomerinundatie een stimulerend effect op het voorkomen van met name de *Lolio-Potentillion*-, de *Phragmitetea*- en de *Bidention*-soorten. In het niet-overspoelde deel van de transecten namen de *Molinio-Arrhenatheretea*-soorten toe, ten gevolge van de hoge neerslag in juli; de meeste soorten die in de natte zomer een toename vertoonden, namen in het hieropvolgende, drogere groeiseizoen het jaar daarop weer af.
In het eurysaleutische gebied met zijn grotere hydrologische dynamiek

en diepere overstromingen blijken juist de zomers met een relatief geringe totale overstromingsduur een gunstige uitwerking te hebben op het voorkomen van een groot aantal soorten. In dergelijke jaren nemen de soorten toe die kenmerkend zijn voor de *Arrhenatheretalia*, de *Bidentetalia*, de *Artemisietea*, de *Chenopodietea*, het *Nanocyperion (Eleocharitetum soloniensis)* en de *Plantaginetea*. In jaren met een langdurige overstroming nemen deze soorten weer af. Het gaat hierbij voornamelijk om soorten met een pionierkarakter, die het ongunstige jaargetijde als zaad doorbrengen (therofyten).In jaren met langdurige zomeroverstroming is de lengte van het groeiseisoen na de laatste inundatie onvoldoende voor een goede ontwikkeling van deze soorten. De soorten van de *Molinio-Arrhenatheretea*, die in het algemeen overstromingsgevoelig zijn, komen in het eurysaleutische milieu bij hoge waterstand geheel onder water en gaan daar dan ook achteruit. Hier vinden wij dus een duidelijke tegenstelling met de situatie in het onderzochte stenosaleutische milieu.

Het gedrag van de soorten, kenmerkend voor het Zilverschoonverbond, is niet eenduidig. De totale bedekking in het transect van de meeste *Lolio-Potentillion*-soorten vertoonde geen correlatie met de schommelingen in de hydrologie. Enkele soorten vormen hierop een uitzondering. De bedekking van *Mentha pulegium* neemt duidelijk af in "natte" jaren, en weer toe in "droge" jaren. *Alopecurus geniculatus* en *Trifolium fragiferum* namen in bedekking af na de langdurige overstroming in de zomer van 1980. Een lange zomerinundatie werkt daarentegen bevorderend op het voorkomen van *Juncus compressus*.

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A key for the identification of the lower units of the LOLIO-POTENTILLION ANSERINAE R.Tüxen 1947 in the northern part of the Atlantic Domain.

The *Lolio-Potentillion anserinae* is characterized by the presence of the character-species *Agrostis stolonifera*, *Alopecurus geniculatus*, *Rumex crispus*, *Juncus inflexus* and the constant companion *Poa trivialis*. Besides the *Plantaginetea* species *Potentilla anserina*, *Plantago major*, *Lolium perenne* and *Poa annua* are present often with high presence degree in most or in some of its communities. The species given in the key are character- and positive differential species. As type relevés of the subassociations have not been presented before, they are given at the end of this key.

Character- and positive differential species of the syntaxonomical units in the *Lolio-Potentillion anserinae*

1. *Potentilla reptans*, *Carex hirta*, *Rorippa sylvestris*, *Juncus compressus*, *Inula britannica*, *Mentha pulegium*, *Phalaris arundinaeea*, *Polygonum amphibium*, *Taraxacum officinale* group , *Elymus repens*, *Lysimachia nummularia*, *Myosotis scorpioides*, *Rorippa amphibia*, *Alopecurus pratensis*, *Equisetum palustre*, *Glechoma hederacea*, *Glyceria maxima*; fresh, eurysaleutic habitat.

RANUNCULO-ALOPECURETUM GENICULATI Tx. 1937

2. *Eleocharis uniglumis*, *Carex otrubae*, *Phragmites australis*; hydrology is less dynamic; fresh or brackish, mainly stenosaleutic habitats.

ASSOCIATION GROUP WITH ELEOCHARIS UNIGLUMIS

RANUNCULO-ALOPECURETUM GENICULATI

1.*Rorippa sylvestris*, *Elymus repens*, *Potentilla reptans*;low ground water table and a dry top soil after the retreat of the inundation water.

Subassociation *rorippetosum sylvestris* Sýkora 1982

Without these characteristics.....2

2. *Equisetum palustre*, *Trifolium repens*, *Cardamine pratensis*, *Equisetum fluviatile*. The water table is close to the soil surface during the greater part of the year.

Subassociation *equisetetosum palustris* Sýkora 1982

Floristic combination and hydrological conditions intermediate between 1 and 2.

Subassociation *typicum* Sýkora 1982

ASSOCIATION GROUP WITH ELEOCHARIS UNIGLUMIS

1. *Nasturtium microphyllum*, *Apium nodiflorum*. Soil water-saturated throughout the year.

Nasturtio-Alopecuretum geniculati Sýkora 1982

1a. *Ranunculus sceleratus*, *Veronica catenata*, *Ranunculus sardous*, *Potentilla anserina*, *Plantago major*, *Eleocharis uniglumis*; nutrient-rich, basic soils.

Subassociation *ranunculetosum scelerati* Sýkora 1982

2a. *Stellaria alsine*, *Holcus lanatus*; less nutrient-rich, moderately acid soils.

Subassociation *stellarietosum alsinis* Sýkora 1982

Without both species.....2

2. *Triglochin palustris*, *Juncus articulatus*, *Galium palustre*, *Ranunculus flammula*, *Hydrocotyle vulgaris*, *Carex nigra*, *Myosotis laxa* ssp. *caespitosa*; moderately acid soils with a low nutrient status. Sensitive to fertilization.

Triglochino-Agrostietum stoloniferae Konczak 1968

2a. *Ranunculus repens*, *Lolium perenne*;fresh soils.

Subassociation *ranunculetosum repentis* Sýkora 1982

2b. *Juncus gerardi*, *Glaux maritima*; slightly brackish soils.

Subassociation *junoetosum gerardii* Sýkora 1982

2c. Species-poor, differential species absent; disturbed by heavy grazing and trampling; also found under conditions too dry for normal development of the association.

Subassociation *inops* Sýkora 1982

Without this species combination.....3

3. *Trifolium fragiferum*, *Juncus gerardi*, *Glaux maritima*, *Carex distans*, *Centaurium pulchellum*; brackish soils.

Agrostio-Trifolietum fragiferi Sýkora 1982

3a. *Plantago major*, *Phragmites australis*, *Drepanocladus aduncus*, *Poa trivialis*, *Carex otrubae*,*Samolus valerandi*, *Lotus tenuis*, *Bellis perennis*; on slightly brackish soils out of reach of the sea.

Subassociation *typicum* Sýkora 1982

3b. *Festuca rubra*, *Holcus lanatus*, *Poa pratensis*, *Plantago coronopus*, *Odontites verna* ssp. *serotina*, *Plantago maritima*, *Cerastium fontanum*, *Centaurium litorale*; slightly higher salt content compared to the subassociation *typicum*. Inundated by sea water during high water spring tides.

Subassociation *festucetosum rubrae* Sýkora 1982

3c. Negatively characterized by the absence or low presence of the differential species of the other subassociations and of *Carex distans*, *Leontodon autumnalis*, *Triglochin maritima*, *Trifolium fragiferum* and *Centaurium pulchellum*. Inundated by sea water during extreme high tide. Characterized by very low grazing pressure.
Subassociation *inops* Sýkora 1982

Communities which cannot be assigned to any of the associations because of the lack of characteristic taxa of the lower units.....4

4. *Festuca arundinacea* occurring with high presence and high coverage 5
No preponderance of *Festuca arundinacea*.....6

5. Derivate community of *Festuca arundinacea*-[*Lolio-Potentillion*].
Irregularly grazed pastures.

5a. *Lolium perenne*, *Elymus repens*, *Ranunculus acris*, *Urtica dioica*;considerably drier soil during the growth season than 5b.
Lolium perenne- type

5b. *Trifolium repens*, *Ranunculus repens*, *Plantago major*, *Alopecurus geniculatus*, *Taraxacum officinale* group, *Carex hirta*, *Eleocharis uniglumis*, *Nasturtium microphyllum*, *Eleocharis palustris*, *Glyceria fluitans*.
Alopecurus geniculatus-type

6. Basal community of *Agrostis stolonifera*-[*Lolio-Potentillion*].
Developing under influence of an increase of the environmental (mostly anthropogenic) dynamics resulting in the disappearance of sensitive species.

6a. *Trifolium fragiferum*, *Ranunculus sardous*, *Juncus gerardi*, *Festuca arundinacea;* brackish, nutrient-rich, wet soils under the influence of intensive grazing, herbicides and/or overfertilization.

Trifolium fragiferum-Ranunculus sardous-type

6b. *Scirpus maritimus*.

Conditions comparable to 6a, but the disturbance is more severe.

Scirpus maritimus-Juncus bufonius-type

6c. *Juncus inflexus*, *Rumex obtusifolius*, *Elymus repens*.

Nutrient-rich, basic soils with a rather dry top soil during summer.

Juncus inflexus-Rumex obtusifolius-type

6d. *Juncus effusus*, *Holcus lanatus*.

Moderately acid soils with a relatively low nutrient status and a moist top soil even in summer.

Juncus effusus-Holcus lanatus-type

6e. *Carex otrubae*, *Eleocharis uniglumis*, *Taraxacum officinale*, *Festuca pratensis*, *Glyceria fluitans*, *Oenanthe fistulosa*, *Bromus racemosus*; soggy, heavy clay soil, irregularly grazed by horses.

Eleocharis uniglumis-Carex otrubae-type

6f. *Juncus inflexus*, *Equisetum palustre*, *Carex otrubae*, *Phragmites australis*, *Mentha aquatica;* severely poached.

Juncus inflexus-Carex otrubae-type

6g. *Carex hirta*, *Trifolium fragiferum;* severely poached and use of herbicides.

Trifolium fragiferum-Carex hirta- type

Type relevés of the subassociations described. Apart from the Irish relevé, all releveś have been made in the Netherlands.

1. *Ranunculo-Alopecuretum geniculati.*
1a.Subassociation *rorippetosum sylvestris.*
Locality: river foreland near Ewijk; pasture, steep slope near water pool;
Exposition: East;
Date: 6th of June 1979;
Size: 8 m^2; total cover: 95 %; height: 20 cm;
Soil type: sandy clay.
Agrostis stolonifera 1, Alopecurus geniculatus 1, Rumex crispus +, Poa trivialis 2a, Potentilla anserina +, Plantago major 1, Poa annua 1, Potentilla reptans 3, Rorippa sylvestris 2a, Elymus repens 1, Carex hirta +, Phalaris arundinacea +, Polygonum amphibium +, Taraxacum officinale +, Lysimachia nummularia +, Ranunculus repens 1, Trifolium fragiferum 1, Coronopus squamatus +, Leontodon autumnalis +, Trifolium pratense +, Trifolium repens +, Atriplex hastata +.

1b.Subassociation *equisetetosum palustris.*
Locality: Horstermeerpolder;moist lower part of a pasture;
Date: 20th of June 1978;
Size: 9 m^2; total cover: 100 %; height: 20-40 cm;
Soil type: clay, rich in organic matter.
Agrostis stolonifera 4, Alopecurus geniculatus 1, Poa trivialis 2a, Carex hirta 1, Polygonum amphibium 2a, Equisetum palustre 2b, Trifolium repens +, Cardamine pratensis +, Equisetum fluviatile +, Ranunculus repens +, Juncus articulatus +, Glyceria fluitans +, Glyceria maxima +, Holcus lanatus +, Festuca pratensis +.

2. *Nasturtio-Alopecuretum geniculati.*
2a. Subassociation *ranunculetosum scelerati.*
For the type relevé see publication 2, page 80.

2b. Subassociation *stellarietosum alsinis.*
Locality: River Barrow near Whitechurch, Co.Waterford, Ireland;sloping

bank of a ditch;
Date: 12th of July 1979;
Size: 4 m^2; total cover: 100 %; height: 15-60 cm;
Soil type: water saturated, very soft clay; poached.
Agrostis stolonifera 4, Alopecurus geniculatus 1, Rumex crispus +, Poa trivialis 2b, Plantago major +, Elymus repens +, Nasturtium microphyllum +, Apium nodiflorum 2a, Stellaria alsine +, Carex otrubae +, Ranunculus repens 2a, Trifolium repens 1, Galium palustre 1, Juncus effusus +, Epilobium parviflorum +, Cirsium arvense +, Senecio aquaticus +, Polygonum hydropiper +, Myosotis laxa ssp.*caespitosa +, Phleum pratense +, Rumex obtusifolius +, Urtica dioica +, Iris pseudacorus +*

3. *Triglochino-Agrostietum stoloniferae*
3a. Subassociation *ranunculetosum repentis.*
Locality: Schiermonnikoog, lower part of a pasture;
Date: 10th of September 1979;
Size: 3 m^2; total cover: 100 %; height: 15-30 cm;
Soil type: a layer of peaty sand on reduced sand; poached.
Agrostis stolonifera 2b, Alopecurus geniculatus 2b, Rumex crispus +, Poa trivialis 2m, Potentilla anserina 2b, Triglochin palustris +, Juncus articulatus 1, Galium palustre 1, Ranunculus flammula 1, Hydrocotyle vulgaris 2b, Carex nigra 1, Myosotis laxa ssp. *caespitosa +, Ranunculus repens 3, Lolium perenne +, Leontodon autumnalis 1, Eleocharis palustris 2m, Cardamine pratensis 1, Glyceria fluitans 1, Rumex acetosa +, Festuca rubra 2m, Juncus conglomeratus +, Phragmites australis 1, Taraxacum officinale +, Poa pratensis 1.*

3b. Subassociation *juncetosum gerardii.*
Locality: Westerplas, Schiermonnikoog;
Date: 12th of September 1979;
Size: 2.25 m^2; total cover: 80 %; height: 5-10 cm;
Soil type: peaty soil on sand.
Agrostis stolonifera 2b, Potentilla anserina 3, Triglochin palustris 1, Juncus articulatus 2m, Galium palustre +, Ranunculus flammula 1, Hydrocotyle vulgaris 1, Carex nigra +, Myosotis laxa ssp. *caespitosa +, Juncus gerardi 2a, Glaux maritima 1, Sagina procumbens +, Trifolium repens 1,*

Odontites verna ssp. *serotina* +, *Mentha aquatica* +, *Phragmites australis* +, *Juncus bufonius* 1, *Cardamine pratensis* +, *Leontodon autumnalis* +, *Poa pratensis* +, *Holcus lanatus* +, *Calliergonella cuspidata* 3.

3c. Subassociation *inops*.
Locality: Ameland;
Date: 31th of July 1978;
Size: 2 m^2, total cover: 100 %; height: 10-20 cm;
Soil type: 12 cm peaty soil on sand.
Agrostis stolonifera 4, *Alopecurus geniculatus* 2a, *Potentilla anserina* 2a, *Juncus articulatus* +, *Galium palustre* 1, *Ranunculus flammula* 1, *Hydrocotyle vulgaris* 1, *Carex nigra* 3, *Juncus effusus* +, *Veronica scutellata* +, *Eleocharis palustris* 1, *Stellaria palustris* +, *Trifolium repens* +, *Agrostis canina* +, *Cardamine pratensis* +, *Brachythecium rutabulum* 1, *Calliergonella cuspidata* 1.

4. *Agrostio-Trifolietum fragiferi*.
4a. Subassociation *typicum*.
Locality: Anna Friso, Noord-Beveland;
Date: 27th of July 1978;
Size: 9 m^2; total cover: 98 %;height: 10-35 cm;
Soil type: 5 cm peaty soil on grey reduced sand.
Agrostis stolonifera 4, *Poa trivialis* 1, *Plantago major* +, *Lolium perenne* +, *Poa annua* 1, *Trifolium fragiferum* 3, *Juncus gerardi* 3, *Glaux maritima* 1, *Carex distans* 2a, *Centaurium pulchellum* 1, *Phragmites australis* 1, *Drepanocladus aduncus* 4, *Carex otrubae* +, *Samolus valerandi* 1, *Lotus tenuis* +, *Bellis perennis* +, *Trifolium repens* 2b, *Festuca arundinacea* 2b, *Triglochin maritima* +, *Scirpus maritimus* +, *Ononis spinosa* +, *Juncus articulatus* +, *Leontodon autumnalis* +, *Brachythecium rutabulum* +.

4b. Subassociation *festucetosum rubrae*.
Locality: De Groede, Terschelling, depression in higher salt marsh zone beneath *Ononido-Caricetum distantis* Runge 1966;
Date: 19th of July 1978;
Size: 2 m^2; total cover: 100 %; height: 5-10 cm;

Soil type: 10 cm peaty soil on sand.
Agrostis stolonifera 3, Potentilla anserina 1, Trifolium fragiferum 2a, Juncus gerardi 3, Glaux maritima 1, Centaurium pulchellum 1, Festuca rubra 3, Holcus lanatus +, Poa pratensis 1, Plantago coronopus +, Odontites verna ssp. *serotina 1, Cerastium fontanum +, Centaurium litorale +, Eleocharis uniglumis 1, Sagina procumbens +, Trifolium repens 3, Linum catharticum +, Brachythecium rutabulum 1.*

4c.Subassociation *inops*.
Locality: Terschelling, depression in higher salt marsh; ungrazed, surrounded by a stand of *Calamagrostis epigejos* (dominant) and *Schoenus nigricans* (co-dominant);
Date: 20th of July 1978;
Size: 9 m^2; total cover: 100 %; height: 20-40 cm;
Soil type: 10 cm peaty soil on grey reduced sand.
Agrostis stolonifera 2b, Glaux maritima 1, Eleocharis uniglumis 2a, Phragmites australis 2m, Galium palustre +, Carex arenaria +, Brachythecium rutabulum 1, Potentilla anserina 4, Juncus gerardi 3.

PUBLICATION I

A revision of the nomenclatural aspects of the *Agropyro-Rumicion crispi*, Nordhagen 1940

by Karel V. Sýkora

Division of Geobotany, Catholic University of Nijmegen, the Netherlands

Communicated by Prof. V. Westhoff at the meeting of June 21, 1980

The name that can be named is not the eternal name.
Lao Tsu, 6th century BC.

SUMMARY

According to the code of Phytosociological Nomenclature the *Agropyro-Rumicion crispi* Nordhagen 1940 proved to be the only correct name for the *Elymus-Honckenya* communities discused by Tüxen in 1966. This alliance is based on the validly published association *Agropyretum repentis maritimum*. As this name is illegitimate, it should be replaced by the next recent name, the *Atriplici-Elymetum arenarii* (Nordh. 1940) Dahl and Hadač 1941. A lectotype has been chosen from the table published by Nordhagen in 1940. The great difference in floristic composition and habitat between the *Ranunculo-Alopecuretum geniculati* (Tx. 1937) (syn. Rumici-Alopecuretum geniculati Tx. 1950) and the *Atriplici-Elymetum arenarii* is shown. The *Ranunculo-Alopecuretum* is transferred to the alliance *Lolio-Potentillion anserinae* in which Tüxen placed this association in 1947. Since he based the name *Ranunculo-Alopecuretum* only on a synoptic table, a neotype is given in this paper.

The first valid publication of the name *Agropyro-Rumicion crispi* was in 1940 in a paper by Nordhagen entitled: "Studien über die maritime Vegetation Norwegens." In this paper he described some plant communities occurring on heaps of seaweed along the Norwegian coast. He placed the *Agropyro-Rumicion crispi* together with the alliance *Polygono-Chenopodion polyspermi* W. Koch 1926 and the *Atriplicion litoralis* Nordhagen 1940, into the *Chenopodietalia* Braun-Blanquet 1936.

Within the *Agropyro-Rumicion* Nordhagen distinguished two associations: the *Convolvuletum sepii maritimum* and the *Agropyretum repentis maritimum*. According to the Code of Phytosociological Nomenclature (Barkman et al. 1976) both names should be rejected because Nordhagen used a geographical

epithet (art. 34). These names are therefore illegitimate but since they have been validly published the name of the alliance is equally valid. In 1950 Tüxen placed the *Convolvuletum sepii maritimum* into the alliance *Convolvulo-Archangelicion litoralis* Tx. 1950 prov., order *Convolvuletalia sepii* Tx. 1950, class *Artemisietea vulgaris* Lohm., Prsg., Tx. 1950.

In 1947 Tüxen published relevés of the *Potentilla anserina-Alopecurus geniculatus* association. As this name is a synonym of the *Ranunculus repens- Alopecurus geniculatus* association, Tx. 1937, it is illegitimate. The same also applies to the *Ranunculetum repentis* Knapp 1946, the *Lolio-Potentilletum anserinae* Knapp 1948 and the *Rumici-Alopecuretum geniculati* Tx. 1950 (*Rumex crispus-Alopecurus geniculatus* association Tx. 1950) for which the only valid and legitimately published name is *Ranunculo-Alopecuretum geniculati* Tx. 1937 (*Ranunculus repens-Alopecurus geniculatus* association Tx. 1937). As Tüxen did not designate the nomenclatural type and his original diagnosis only consists of a synoptic table I herewith publish a neotype (table 1).

Table 1. Comparison of 1) *Agropyretum repentis maritimum* Nordhagen 1940 (46 relevés); 2) *Elymus -Agropyron repens* sociation (4 relevés); 3) *Atripliceto-Elymetum arenarii* (Nordhagen 1940) Dahl and Hadač 1941 as published in Tx. 1966 (26 relevés); 4) *Ranunculus repens-Alopecurus geniculatus* association Tx. 1937 (6 relevés); 5) *Potentilla anserina-Alopecurus geniculatus* association Tx. 1947 (1 relevé); 6) Neotype of the *Ranunculo-Alopecuretum geniculati* Tx. 1937. Locality: River forelands of Neder-Rijn (Rhine) near Amerongen; date: 20th of June 1979; author: K.V. Sýkora; size: 18 m^2; total cover 100%; height: lower herb layer 35 cm, higher field layer 100 cm, moss layer absent; soil type: clay.

	1	2	3	4	5	6
Elytrigia repens (L.) Desv.	V	V	IV			+
Potentilla anserina L.	V	IV	IV	III	+	
Rumex crispus L.	IV	IV	II	II	+	2a
Sonchus arvensis L.	IV	V	IV			
Atriplex littoralis L.	III	IV	IV			
Atriplex hastata L.	III	III	III			
Elymus arenarius L.	II	V	V			
Artemisia vulgaris L.	II	IV	III			
Festuca rubra L.	II	IV	II			
Honckenya peploides Ehrh.	I	V	II			
Plantago maritima L.	II	III	II			
Vicia cracca L.	III	III	II			
Silene maritima With.	II	III	II			
Galeopsis bifida Boenningh.	III	III	I			
Galium aparine L.	III	II	I			
Lotus corniculatus L.	I	III	I			
Leontodon autumnalis L.	I	III	I	III		
Euphorbia palustris L.	I	II	I			
Cakile maritima Scop.	II	II	I			
Matricaria maritima L.	III	II				
Linaria vulgaris Mill.	II	III				

	1	2	3	4	5	6
Carex arenaria L.	II	III	I			
Galium verum L.	II	III				
Arrhenatherum elatius (L.) P.B. ex J. et C. Presl.	II	II	I			
Anthriscus sylvestris Hoffm.	II	II	I			
Achillea millefolium L.	I	III				
Pimpinella saxifraga L.	I	III				
Stachys palustris L.	I	II	I			
Ammophila arenaria (L.) Link	I	II				
Lathyrus maritimus Bigelow	I	II	I			
Phragmites australis (Cav.) Trin. ex Steud.	I	II	I		+	
Plantago lanceolata L.	I	II	I			
Sedum acre L.	I	II				
Valeriana officinalis L.	I	II				
Poa pratensis L.	I	II		III		
Melilotus albus Desr.	I		III			
Aster tripolium L.	I		II			
Taraxacum officinale Web. ex Wigg.	II		I			+
Angelica archangelica L. ssp. litoralis Th.	I		I			
Plantago major L.	I		I		+	+
Polygonum aviculare L.	I		I			
Glaux maritima L.	I		I			
Cochlearia officinalis L.	I		I			
Tussilago farfara L.	I		I			
Cirsium vulgare (Savi) Ten.	II		I			
Agrostis stolonifera L.	II		I			2a
Cirsium arvense (L.) Scop.	II					
Melilotus altissimus Thuill.	II					
Centaurea jacea L.	II					
Senecio viscosus L.	II					
Equisetum arvense L.	I				+	
Poa trivialis L.	I				+	2b
Festuca pratensis Huds.	I		I	I		2a
Trifolium repens L.	I			III	(+)	+
Ranunculus repens L.				V	4	2a
Alopecurus geniculatus L.				V	3	2a
Galium palustre L.				V	+	+
Ranunculus flammula L.				V		
Carex otrubae Podp. (vulpina L. var.)				III		+
Lysimachia nummularia L.				III	+	2a
Glyceria fluitans (L.) R. Br.				III	1	2m
Mentha aquatica L.				III	+	
Myosotis scorpioides L.				III		+
Stellaria palustris Retz.				III		
Oenanthe fistulosa L.				III		
Phalaris arundinacea L.				II	+	+
Eleocharis palustris (L.) R. et Sch.				II	2	2b
Cardamine pratensis L.				II		1
Caltha palustris L.				II		
Senecio aquaticus Huds.				II		
Lychnis flos-cuculi L.				II	+	
Alopecurus pratensis L.				II		

	1	2	3	4	5	6
Carex ovalis Good.				II		
Agrostis tenuis Sibth.				II		
Potentilla reptans L.				I		+
Rorippa sylvestris (L.) Besser					+	
Calliergonella cuspidata (Hedw.) Loesk.					2	
Galium uliginosum L.					+	
Polygonum amphibium L. f. terrestre					+	
Drepanocladus aduncus (Hedw.) Warnst.					1	
Typha latifolia L.					+	
Alisma plantago-aquatica L.					+	
Juncus bufonius L.					+	
Scirpus sylvaticus L.					+	
Lythrum salicaria L.					+	
Trifolium pratense L.					(+)	
Lolium perennne L.						1
Cerastium holosteoides Fr.						1
Juncus articulatus L.						+
Geranium dissectum L.						+

Besides in column 1: *Trifolium pratense* L., *Glechoma hederacea* L., *Stellaria media* (L.) Vill., *Achillea ptarmica* L., *Geranium pratense* L., *Angelica sylvestris* L., *Carum carvi* L., *Dactylis glomerata* L., *Filipendula ulmaria* (L.) Maxim., *Heracleum sibiricum* L., *Lythrum salicaria* L., *Rumex domesticus Hartm., Convolvulus sepium* L., *Tanacetum vulgare* L., *Asparagus officinalis* L., *Urtica dioica* L., *Senecio vulgaris* L., *Cynoglossum officinale* L., *Solanum nigrum* L., *Chenopodium album* L., *Sisymbrium sophia* L., *Salsola kali* L., *Atriplex laciniata* L., *Glaucium flavum Crantz, Elytrigia junceiformis A. et D. Löve, Polygonum nodosum Pers., Geranium sanguineum* L., *Ononis arvensis* L., *Stellaria crassifolia Ehrh., Medicago lupulina* L., *Sedum telephium* L. ssp. maximum (L.) Krocker; in column 3: *Festuca rubra* L. ssp. arenaria Richter, *Statice bahusiensis Fries, Stellaria media* (L.) Vill., *Elytrigia junceiformis A. et D. Löve, Calystegia sepium R. Br., Galeopsis tetrahit* L., *Rumex domesticus Hartm., Hieracium umbellatum* L., *Haloscias scoticum* L., *Mertensia maritima Gray, Puccinellia maritima Parl., Tripleurospermum maritimum Koch., Vicia sepium* L., *Cakile maritima Scop.;* in column 4: *Deschampsia caespitosa* (L.) Pal., *Lotus uliginosus Schkuhr., Anthoxanthum odoratum* L., *Phleum pratense* L., *Bellis perennis* L., *Trifolium dubium Sibth.*, all with presence class I.

In 1947 Tüxen placed the *Ranunculo-Alopecuretum geniculati* Tx. 1937 into the new alliance *Lolio-Potentillion anserinae.* In 1950 however Tüxen restored the name *Agropyro-Rumicion* mentioning the *Potentillion* as its synonym. In the same paper he combined the *Ranunculo-Alopecuretum geniculati* Tx. 1937 and the *Agropyretum repentis maritimum* Nordhagen 1940 with some other associations in the alliance *Agropyro-Rumicion crispi* Nordhagen 1940. As he removed the *Convolvuletum sepii maritimum* from the *Agropyro-Rumicion,* the only remaining association in Nordhagen's table, the *Agropyretum repentis maritimum,* becomes the lectotype on which the alliance is based.

In 1966 Tüxen described the nitrophilous *Elymus-* communities which occur along the coasts af the northern part of Japan, Europe and America, distinguishing four associations, the *Potentillo-Elymetum arenarii* (sub nom. *Potentillo-Elymetum arenariae* (Raunkiaer 1935) Tx. 1966); the *Soncho brachyotis-*

Elymetum mollis Tx. 1966; the *Honckenyo robustae-Elymetum villosi* Fernandez 1959 and the *Elymo-Festucetum arenariae subarcticum* (Regel) Nordhagen 1955. He proposed to group these *Elymus-Honckenya* communities into the *Honckenyo-Elymion arenarii* (sub nom. *Honckenyo-Elymion arenariae*) (Fernandez-Galiano 1954) Tx. 1966, the *Honckenyo-Elymetalia arenarii* (sub nom. *Honckenyo-Elymetalia arenariae* Tx. 1966) and the *Honckenyo-Elymetea arenarii* (sub nom. *Honckenyo-Elymetea arenariae*) Tx. 1966.

Concerning the *Potentillo-Elymetum arenarii* Tüxen wrote (translation by the present author): "We still do not dare to decide whether the *Potentillo-Elymetum arenarii* could stay in the *Agropyro-Rumicion,* like the *Crambeetum* and the *Halosciadetum scotici.* There is something to be said for putting this association into the *Honckenyo-Elymion arenarii,* to which we also account the American *Arenario robustae-Elymetum villosi* Fern.-Gal. 1959, the Japanese *Soncho-Elymetum mollis* and the *Elymo-Festucetum arenariae* (Regel) Nordhagen 1955 and the corresponding Canadian communities." The name *Potentillo-Elymetum arenarii* should be rejected because of the principle of priority. Raunkiaer's name, *Elymus arenarius* formation (1935) cited by Tüxen is invalid; the name *Agropyretum repentis* Nordhagen 1940 however has been validly published. Being illegitimate it must be replaced by the more recent name, in this case the *Atriplici-Elymetum arenarii* (Nordhagen 1940) Dahl and Hadač 1941. The names published before 1940 are not valid because the original diagnosis was insufficient (Andersen 1910, Regel 1928, Regel 1938), or they are nomina dubia (Regel 1928, Steindórsson 1936) or because they have been published for naming a sociation (Störmer 1938) or formation (Raunkiaer 1935). As a lectotype for the *Atriplici-Elymetum arenarii* (Nordhagen 1940) Dahl and Hadač 1941, I chose relevé number 45 from the table of the *Agropyro-Rumicion crispi* published by Nordhagen in 1940. If all the *Elymus-Honckenya* communities described by Tüxen (1966) belong to one alliance, then, to the opinion of the present author, they all belong to the *Agropyro-Rumicion crispi.*

In table 1, the synoptic table of the *Ranunculus repens-Alopecurus geniculatus* association Tx. 1937, the relevé of the *Potentilla anserina-Alopecurus geniculatus* association Tx. 1947 and the neotype of the *Ranunculo-Alopecuretum geniculati* are compared with the synoptic tables of the *Agropyretum repentis maritimum* Nordhagen 1940, the *Elymus- Agropyron repens* sociation Nordhagen 1940 and the *Potentillo-Elymetum* (Raunkiaer 1935) Tx. 1966. Although *Potentilla anserina* and *Rumex crispus* are present in both groups, the great difference in their floristic composition is immediately apparent. *Sonchus arvensis, Atriplex litorale, Atriplex hastata, Elymus arenarius, Artemisia vulgaris, Festuca rubra, Honckenya peploides, Plantago maritima, Vicia cracca, Silene maritima, Galeopsis bifida, Galium aparine, Galium verum, Achillea millefolium, Pimpinella saxifraga* and *Melilotus albus* have a high presence (III or more) in at least one of the *Elymus* communities and are totally absent in the *Ranunculo-Alopecuretum.* On the other hand species absent from

the *Elymus* communities but with a high presence in the *Ranunculo-Alopecuretum* are: *Ranunculus repens, Alopecurus geniculatus, Ranunculus flammula, Galium palustre, Carex otrubae* (*C. vulpina* L. var.), *Lysimachia nummularia, Glyceria fluitans, Mentha aquatica, Myosotis scorpioides, Stellaria palustris, Oenanthe fistulosa* and some species with presence degree II. Recent research (37 relevés unpublished) adds the following species to this list: *Carex hirta* L. (presence class IV), *Rorippa sylvestris* L. Besser (III), *Potentilla reptans* L. (III), *Juncus compressus* Jacq. (II), *Poa annua* L. (III), *Polygonum amphibium* L. f. *terrestre* and *Eleocharis palustris* (III). Besides *Agrostis stolonifera* (V), *Poa trivialis* (V) and *Trifolium repens* (III) have much higher presence degrees. In his synoptic table of the *Ranunculus repens-Alopecurus geniculatus* association Tx. 1937, Tüxen mentioned *Carex vulpina* L. var. As *Carex otrubae* Podp. has been known as *Carex vulpina* L. var. *nemorosa* and as it has often been confused with Carex vulpina L. (Oberdorfer 1970, de Langhe 1978), I consider this to be the species which Tüxen meant in 1937 (see table 1). As is to be expected there are also considerable differences in habitat. The Agropyro-Rumicion crispi that Nordhagen described was observed on old heaps of seaweed, consisting purely of organic material, and on sandy, gravelly or stoney soils rich in organic materials. Their moisture content varied from slightly moist to dry and the covering vegetation varied from hardly grazed to ungrazed.

The *Ranunculo-Alopecuretum geniculati* occurs on heavy nutrient-rich soils, on riverbanks, along former river beds, beside pools resulting from dike bursts, in or along depressions containing stagnant water, at the edge of drinking pools for cattle and along ditches. The intensively grazed vegetation is frequently flooded which causes the soil to be saturated with water and deficient in oxygen for the greater part of the year. Besides its presence is not determined by the occurrence of organic drift material.

CONCLUSION

The great difference in floristic composition and habitat do not justify the combination of the *Atriplici-Elymetum arenarii* (Nordhagen 1940) Dahl and Hadač 1941 and the *Ranunculo-Alopecuretum geniculati* into one alliance. The name *Agropyro-Rumicion crispi* should be used for the alliance containing the type association *Atriplici-Elymetum arenarii*. The first validly published name for the alliance to which the *Ranunculo-Alopecuretum geniculati* belongs is *Lolio-Potentillion anserinae* Tüxen 1947 (Synonym: Agrostion stoloniferae Görs 1966).

Although a proposal to the Nomenclatural Commission to reject the name Agropyro-Rumicion as a nomen ambiguum (art. 36) could be considered, the present author for practical reasons prefers to maintain this name.

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PUBLICATION II

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SYNTAXONOMY AND SYNECOLOGY OF THE LOLIO-POTENTILLION TÜXEN 1947 IN THE NETHERLANDS*

K. V. SÝKORA

Botanisch Laboratorium, Afdeling Geobotanie, Toernooiveld, 6525 ED Nijmegen.

SUMMARY

From 1978 to and including 1980 the author studied Dutch pastures inundated in winter and spring. The ecology and taxonomy of the following communities are described in this paper:
Class: *Plantaginetea majoris* R. Tüxen and Preising 1950
Order: *Agrostietalia stoloniferae* Oberdorfer, Müller and Görs 1967
Alliance: *Lolio-Potentillion anserinae* Tüxen 1947
Ranunculo-Alopecuretum geniculati Tüxen 1937
Subassociations: *typicum* subass.nov.
rorippetosum sylvestris subass.nov.
equisetetosum palustris subass.nov.
Nasturtio-Alopecuretum geniculati ass.nov.
Triglochino-Agrostietum stoloniferae Konczak 1968
Subassociations: *ranunculetosum repentis* subass.nov.
juncetosum gerardii subass.nov.
inops subass.nov
Agrostio-Trifolietum fragiferi ass.nov.
Subassociations: *typicum* subass.nov.
festucetosum rubrae subass.nov.
inops subass.nov.
Derivate community of *Festuca arundinacea-[Lolio-Potentillion]*
Basal community of *Agrostis stolonifera-[Lolio-Potentillion]*
Community of *Scirpus maritimus* and *Alopecurus geniculatus*
Class: *Asteretea tripolii* Westhoff and Beeftink 1962
Order: *Glauco-Puccinellietalia* Beeftink and Westhoff 1962
Alliance: *Armerion maritimae* Braun-Blanquet and De Leeuw 1936
Ononido-Caricetum distantis Runge 1966
Juncetum maritimi Bilik 1956
Besides some comments are made on the *Alopecurus arundinaceus* community, observed in Sweden, which is unclear syntaxonomically. The relation of these communities to one another and to the two major environmental factors – salt influence and the position of the ground-water level during the growing season – are discussed on the basis of an ordination diagram.

1. INTRODUCTION

Because of the great difference in floristic composition and habitat the communities of inundated pastures (*Lolio-Potentillion anserinae* Tüxen 1947) and the communities occurring on organic drift material along the coasts of the northern part of Europe (*Agropyro-Rumicion crispi* Nordhagen 1940), previously

*Dedicated to Prof. V. Westhoff on the occasion of his retirement from the University of Nijmegen.

combined in the *Agropyro-Rumicion crispi* Nordhagen 1940 em.Tüxen 1950, have been separated by SÝKORA (1980).

As the *Lolio-Potentillion* had been studied insufficiently (WESTHOFF & DEN HELD 1969, WILMANNS 1978), a study into the syntaxonomy and synecology of the *Lolio-Potentillion* in some countries of Western Europe was started in 1978. Relevés were made in The Netherlands (1978, 1979 and 1980), Ireland (1979), Belgium and the northern part of France (1980), England and Wales (1981) and South Sweden (1978). In order to study the long term dynamics of the hydrology determining the occurrence of the alliance, permanent transects were investigated during these years. Papers about the data from Ireland, Belgium, France and from the transects are in preparation.

2. METHODS

During the analytical phase 428 relevés were made according to the Braun-Blanquet method (WESTHOFF & VAN DER MAAREL 1973). For estimation of the quantitative occurrence of each species the Braun-Blanquet scale as refined by BARKMAN et al. (1964) was used. The location of the sites visited is shown in *fig. 1*. A few relevés from Sweden have been added to the table (column 29). The size of the sample plots varied from 1 to 25 square meters, most of them being 4 square meters or more. According to various sources (see WESTHOFF & VAN DER MAAREL 1973) the minimal area values for pastures (*Lolio-Cynosuretum*) varies between 5 and 10 sq.m. Very often the shape of the plots was oblong, for instance 2 × 10 or 0.5 × 10 m, parallel to the waterline. The sites were selected using the knowledge already existing in phytosociological literature (e.g. PASSARGE 1964, WESTHOFF & DEN HELD 1969, OBERDORFER 1977, ELLENBERG 1978, RUNGE 1980) about the floristic composition and habitat of the *Lolio-Potentillion* and of the adjacent communities belonging to the alliances found on sites with a different hydrology and management (e.g. *Arrhenatherion, Phragmition, Magnocaricion, Bidention*). No relevés were made of the *Poo-Lolietum* D.M. de Vries and Westhoff n.n. apud Bakker 1965 because this association developing out of the *Lolio-Cynosuretum* when excessive manuring with nitrogen is applied, usually with an increase in grazing intensity, should be assigned to the *Lolio-Plantaginion* (FOERSTER 1968, WESTHOFF & DEN HELD 1969). The *Poo-Lolietum* occurs on sites which are too dry for the *Lolio-Potentillion*.

An auger was used to take soil samples in order to determine the soil texture and the organic material content. Besides grazing and poaching intensity, soil moisture, height above and distance from open water and salt influence were recorded.

In the synthetical phase the Tabord program was used for structuring the rough table (VAN DER MAAREL et al. 1978). The scale of BARKMAN et al. (1964) was transformed according to the ordinal transformation (VAN DER MAAREL 1979a, b). The similarity ratio (WISHART 1969) was used to measure similarities between relevés and clusters. The relevés were divided into two tables. In the

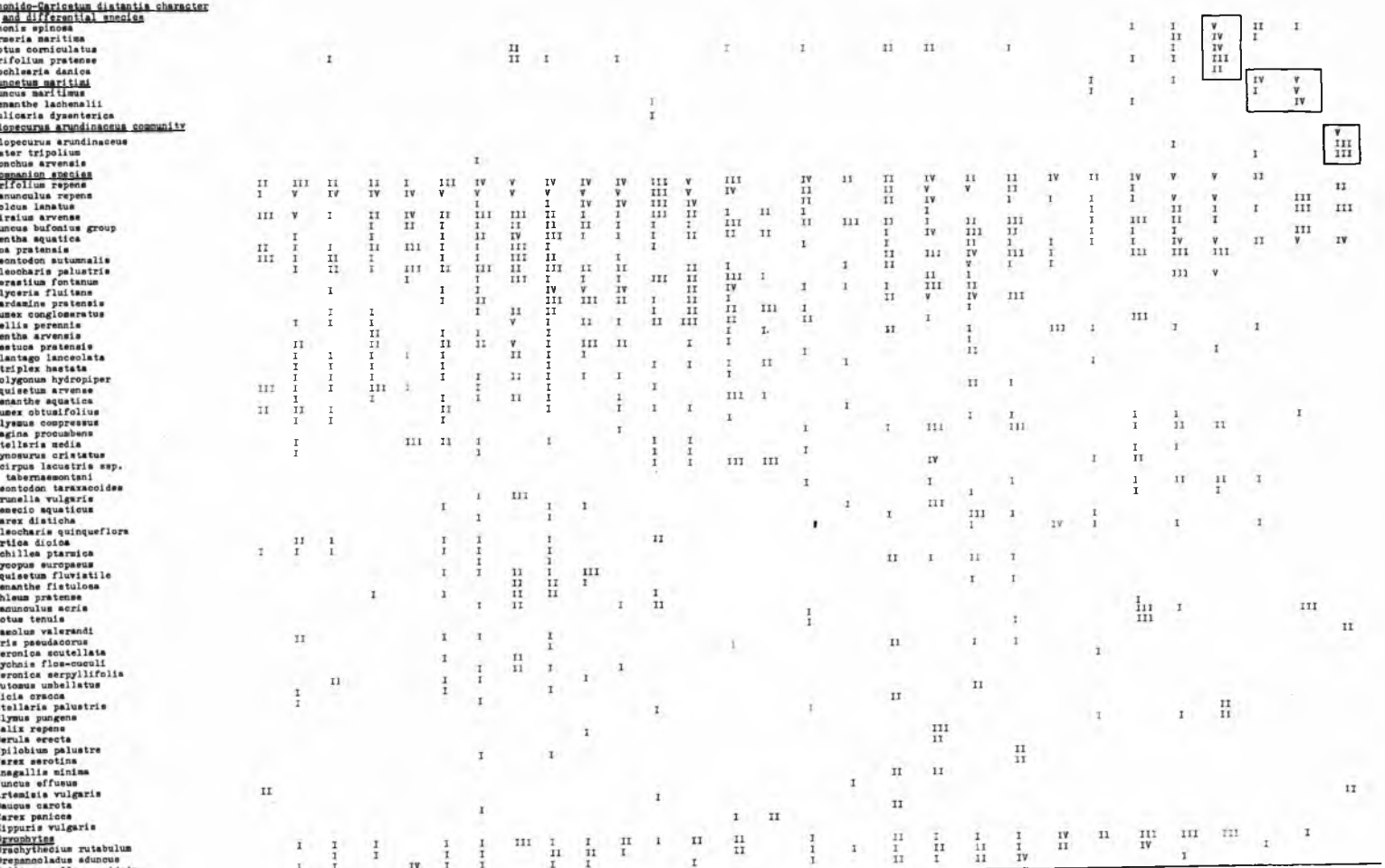
Fig. 1. Map of The Netherlands on which the localities where relevés were made are indicated with an asterix.

Table 1. Synoptic table of communities assigned to the Lolio-Potentillion anserinae Tx. 1947 occurring in The Netherlands as well as some other communities.

1–11 Ranunculo-Alopecuretum geniculati Tx. 1937
1–5 Subass. rorippetosum sylvestris
6 Subass. typicum
7–11 Subass. equisetetosum palustris
12–13 Derivate community of Festuca arundinacea-[Lolio-Potentillion]
14 Nasturtio-Alopecuretum geniculati ass.nov.
15 Community of Scirpus maritimus and Alopecurus geniculatus
16–17 Basal community of Agrostis stolonifera-[Lolio-Potentillion]
18–22 Triglochino-Agrostietum stoloniferae Konczak 1968
18 Subass, inops
19–20 Subass. ranunculetosum repentis
21–22 Subass. juncetosum gerardii
23–25 Agrostio-Trifolietum fragiferi ass.nov.
23 Subass. inops
24 Subass. typicum
25 Subass. festucetosum rubrae

Other communities
26 Ononido-Caricetum distantis Runge 1966
27–28 Juncetum maritimi Bilik 1956
29 Alopecurus arundinaceus community

Table 1. Legend on preceding page.


Juncetum gerardi
Juncetum maritimi
Juncus maritimus
Lolio-Cynosuretum
Lolium perenne
Trifolium repens
Cynosurus cristatus
Bromo-Festucetum rubrae
Festuca rubra
Agrostis stolonifera
Festuca pratensis
Festuca arundinacea
Festuca ovina
Agrostis tenuis
Poa pratensis
Poa trivialis
Holcus lanatus
Anthoxanthum odoratum
Trifolio-Cynosuretum
Trifolium pratense
Trifolium dubium
Lotus corniculatus
Leontodon autumnalis
Centaurea nigra
Rumex acetosa
Ranunculus acris
Ranunculus repens
Cerastium fontanum
Plantago lanceolata
Plantago major
Bellis perennis
Prunella vulgaris
Achillea ptarmica
Leucanthemum vulgare
Glyceria fluitans
Juncus articulatus
Juncus bufonius
Juncus effusus
Juncus inflexus
Juncus conglomeratus
Juncus gerardi
Carex nigra
Carex panicea
Carex flacca
Carex hirta
Carex arenaria
Carex disticha
Carex otrubae
Carex hostiana
Carex pulicaris
Carex viridula
Carex flava
Carex lepidocarpa
Carex demissa
Carex serotina
Carex extensa
Carex distans
Carex arenaria
Carex hostiana
Carex flacca
Carex nigra
Carex panicea
Carex viridula
Carex flava
Carex lepidocarpa
Carex demissa
Carex serotina
Carex extensa
Carex distans
Juncus gerardi
Juncus maritimus
Juncus bufonius
Juncus effusus
Juncus inflexus
Juncus conglomeratus
Glyceria fluitans
Glyceria maxima
Glyceria plicata
Glyceria declinata
Glyceria fluitans
Glyceria maxima
Glyceria plicata
Glyceria declinata
Alopecurus geniculatus
Alopecurus pratensis
Phalaris arundinacea
Phragmites australis
Phragmites australis
Phalaris arundinacea
Alopecurus pratensis
Alopecurus geniculatus
Eleocharis palustris
Eleocharis uniglumis
Eleocharis quinqueflora
Eleocharis multicaulis
Eleocharis multicaulis
Eleocharis quinqueflora
Eleocharis uniglumis
Eleocharis palustris
Scirpus lacustris ssp. tabernaemontani
Scirpus maritimus
Scirpus maritimus
Scirpus lacustris ssp. tabernaemontani
Oenanthe lachenalii
Oenanthe fistulosa
Oenanthe aquatica
Lysimachia vulgaris
Lysimachia nemorum
Lysimachia nummularia
Lysimachia nummularia
Lysimachia nemorum
Lysimachia vulgaris
Ranunculus flammula
Ranunculus lingua
Ranunculus ficaria
Ranunculus ficaria
Ranunculus lingua
Ranunculus flammula
Galium palustre
Galium uliginosum
Galium palustre
Galium uliginosum
Lythrum salicaria
Lythrum portula
Lythrum portula
Lythrum salicaria
Epilobium hirsutum
Epilobium parviflorum
Epilobium hirsutum
Epilobium parviflorum
Mentha aquatica
Mentha arvensis
Mentha arvensis
Mentha aquatica
Lycopus europaeus
Lycopus europaeus
Scutellaria galericulata
Scutellaria galericulata
Myosotis scorpioides
Myosotis scorpioides
Valeriana officinalis
Valeriana officinalis
Angelica sylvestris
Angelica sylvestris
Cirsium palustre
Cirsium palustre
Cirsium arvense
Cirsium arvense
Cirsium vulgare
Cirsium vulgare
Senecio aquaticus
Senecio aquaticus
Senecio jacobaea
Senecio jacobaea
Senecio erucifolius
Senecio erucifolius
Senecio fluviatilis
Senecio fluviatilis
Senecio paludosus
Senecio paludosus
Senecio vulgaris
Senecio vulgaris
Senecio viscosus
Senecio viscosus
Senecio sylvaticus
Senecio sylvaticus
Senecio squalidus
Senecio squalidus
Senecio jacobaea
Senecio aquaticus
Senecio erucifolius
Senecio fluviatilis
Senecio paludosus
Senecio vulgaris
Senecio viscosus
Senecio sylvaticus
Senecio squalidus
Cirsium palustre
Cirsium arvense
Cirsium vulgare
Cirsium palustre
Cirsium arvense
Cirsium vulgare
Cirsium palustre
Cirsium arvense
Cirsium vulgare

Cluster number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
number of relevés	5	16	15	11	7	59	30	4	51	8	14	12	9	16	9	16	17	14	12	11	10	4	28	12	17	14	10	6	4
Plantaginetea + Lolio-Plantaginetum																													
Potentilla anserina	IV	II	IV	IV	II	IV	III	III	III	1	II	III	12	III	III	V	IV	V	III	V	V	V	V	II	V	V	V	IV	III
Plantago major	II	V	IV	III	IV	V	III	V	IV	II	III	II	IV	IV	II	V	II	I	IV	I	II		II	IV	II			I	
Lolium perenne	I	I	I	III	II	II	V	V	II	1	1II	IV	II	I3	II	IV	I		III	II			I	II	I		I		
Poa annua	II	III	IV	II	I	I	III	1II	I	1	II	I	1	I		I	II	I	I	I	I		I	I	I				
Polygonum aviculare	I	1	II	II	I	II	1		1	I				I		I													
Lolio-Potentillion character species + constant companion																													
Agrostis stolonifera	V	IV	IV	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	V	IV	V	V	V	V	V	V	V	V
c.c. Poa trivialis	I	V	IV	III	V	V	V	V	V	V	V	IV	V	V	III	V	I	I	V	III	I	IV	I	III	I			I	
Alopecurus geniculatus		II	V	V	IV	V	III	II	V	IV	V	II	IV	V	IV	IV	V	III	V	IV	I	II	II						
Rumex crispus	V	V	V	V	III	V	V	IV	IV	III	III	III	IV	III	I	I	I	1	I	III			I						V
Carex otrubae						I	I	II	I			II	III	II	II	I	I						I	III				I	
Juncus inflexus						I	I	3I	I			I		I		I													
Ranunculo-Alopecuretum character and differential species																													
Phalaris arundinacea	IV	V	IV	II	II	V	IV	III	III	I	I	I	I	I			I						I						
Polygonum amphibium	II	III	III	I		IV	IV	IV	IV	II	I			I				I	I	II				I					
Potentilla reptans	III	IV	V	IV	V	II	II	III	I		I							I		I	I		I						
Taraxacum officinale group	II	V	III	II	I	113	II	III	II	1	III	I	III	I			I	I		I						I			
Elymus repens	V	V	V	V	V	IV	III	II	II	I	III	IV		I	I	I	I	I	I				I						
Carex hirta	I	I	II	IV	V	II	IV	III	III	II	III		III	II		I	I						I						
Lysimachia nummularia		II	I	I			III	V	III	I			I						II										
Myosotis scorpioides		I	1	II	V	II	1II	IV	V	III	I																		
Rorippa sylvestris	1V	IV	V	II	V	IV	I		II		I																		
Rorippa amphibia		I	12	I	11	III	II	II	II	I			I																
Juncus compressus			I	11	IV	I	II	II	I		I																		
Alopecurus pratensis	I	IV	I	II		II	II		I		I	I																	
Equisetum palustre						II	IV	III	I	IV	II		II	I				I											
Glyceria maxima		II				II	II	III	1																				
Glyceria maxima						I	I	III	IV	IV	I																		
Mentha pulegium					IV																								
Inula britannica						I	I																						
Association group with Eleocharis uniglumis character and differential species.																													
Phragmites australis						I	I		1	1		II	I	II	II	II	I	I	III	V	IV	III	II	IV	II	II	I	IV	III
Eleocharis uniglumis						I			I	I		I	III	III	IV	III	I	II	II	IV	III	III	IV	V	I	III	I	I	
D.c. Festuca arundinacea- Lolio-Potentillion																													
Festuca arundinacea	I	I		I					I			V	V	II	II	III	I	I	III				II	III	II	I	II	V	IV
Rasturtio-Alopecuretum character and differential species																													
Ranunculus sceleratus			I	I	II	I	I		I	I				V	III	II	I		II		I								
Rasturtium microphyllus						I	I		I		I		II	IV	II	I				I									
Veronica catenata		I	I	II	III	II	I	II	II	I	I			IV	II		I			I	I		I						
Ranunculus sardous											I	II	III	III	II	III	I						I						
Epilobium parviflorum									I			I		III	I	I			I					I					
Glyceria declinata											I		I	II					I										
Community of Scirpus maritimus and Alopecurus geniculatus																													
Scirpus maritimus						I						I	II	I	V	II	III		I				II	III			I	I	V
Trigliochino-Agrostietum character and differential species																													
Juncus articulatus			I	I	III	I	I	IV	IV	IV	II	I	II	III		II	II	IV	V	V	V	V	I	III	II	I	I		
Galium palustre			I	I	I	I	II	II	IV	II				I				IV	V	V	IV	II	II	I				I	II
Triglochin palustris						I			I	I			I	II	II	I	II		V	III	II	IV	I	II	II				
Ranunculus flammula							I		I		I			I			I	IV	III	V	III	V			I				
Hydrocotyle vulgaris																		IV	III	V	V	II	I		I	I			
Carex nigra									I					I		I		V		V	V	V	I		II	I	I		
Myosotis laxa ssp.caespitosa			I			I	I	II	I	I	I			I				I	IV	V	III								
Agrostio-Ranunculetum fluitantis character and differential species																													
Juncus gerardi						I						I	I	I	III	III	I	I	II	I	V	V	V	V	V	V	V	IV	
Glaux maritima												I		II	II	II	I	I			IV	V	IV	V	II	V	IV	II	
Trifolium fragiferum				I	I	I		II			I	I	II	II		IV	I	I		I		V	I	V	III	II	I		
Triglochin maritima																I	I		I		I	II		II	II	I	II		II
Carex distans																I	I						I	IV	IV	V	II	IV	
Centaurium pulchellum																	I				II		I	V	III		II		
Agrostio-Trifolietum fragiferi festucetosum rubrae and Ononido-Carlinetum																													
Festuca rubra		I		I								I				I	I	I	I	I			I		V	V	V	V	II
Plantago coronopus																							I	I	III	III			
Odontites verna ssp. serotina									I				I		I						I		II		III	III	III		
Plantago maritima																							I	I	III	III	IV		II
Centaurium litterale																													

definite table the treshold value was 0.35 in both tables, the fusion level 0.67 and 0.77 respectively. After removing the rest group and the clusters clearly belonging to associations from other alliances (*Lolio-Cynosuretum, Sagino maritimae-Cochlearietum danicae*), 401 relevés remained. Only the synoptic table is presented here (*table 1*). Apart from this general table, four synoptic tables of lower units were constructed in order to show their internal structure (*tables 2, 4, 5* and *6*).

The cluster centroids, that is the mean of the transformed cover abundance values of each species belonging to one cluster, were used in a principal components analysis. For this ordination the Ordina program (ROSKAM 1971, see also VAN DER MAAREL 1979a) was used.

Names of phanerogams are according to the Flora Europaea (TUTIN et al. 1964–1980). The mosses are named according to LANDWEHR (1966).

3. RESULTS

3.1 THE ALLIANCE *Lolio-Potentillion* Tüxen 1947.

Synonym: *Agrostion stoloniferae* Görs 1966, *Agropyro-Rumicion crispi* Nordhagen 1940 em. R. Tüxen 1950 pro parte. Non *Agropyro-Rumicion crispi* Nordhagen 1940 (see Sýkora 1980)

Syntaxonomy (*table 1*): The *Lolio-Potentillion* as studied in The Netherlands is characterized by the presence of the character-species *Agrostis stolonifera, Alopecurus geniculatus* and *Rumex crispus,* and the constant companion *Poa trivialis.* Constant companions are species which have a presence of more than 60% but cannot be designated as character-species or differential species (BRAUN-BLANQUET 1925, 1928, 1959, 1964).

Carex otrubae and *Juncus inflexus* are placed under the heading *Lolio-Potentillion* in the table because they have a clear preference for some of the lower units in the Belgian, French and Irish material. In the Dutch material these species do not show any obvious preference. *Lymnaea truncatula* Müll., the liver fluke snail, occurs with preference in the *Lolio-Potentillion* (OVER 1967) as its occurrence is promoted by grazing, ground-water fluctuation and poaching (see Synecology).

In 1970 TÜXEN separated the *Lolio-Plantaginion majoris* Sissingh 1969 and the *Lolio-Potentillion* (called Agropyro-Rumicion in his paper) and put them into separate orders which he placed into the class *Molinio-Arrhenatheretea* Tüxen 1937. Whereas the first alliance remained in the *Plantaginetalia majoris* R. Tüxen (1947) 1950, the *Lolio-Potentillion* was placed into the *Trifolio fragiferi-Agrostietalia* (Oberdorfer 1967 em. Tüxen 1970). In 1971 OBERDORFER abandoned the unit *Lolio-Plantaginetum* (Linkola 1921) Beger 1930 em. Sissingh 1969 (*Lolio-Plantaginion* Sissingh 1969), and after dividing this community into three subassociations, one of which he assigned to the *Cynosurion* (Tüxen 1937), her renamed it the *Matricario-Polygonetum* Müller mscr. In the same paper he stated that *Lolium perenne* is not a character-taxon of the *Plantaginetea majoris* Tüxen et Preising 1950, but of the *Cynosurion.*

In 1972 KRIPPELOVÁ divided the *Lolio-Plantaginetum* into the subassociations *typicum* Krippelová 1972, *poetosum annuae* Krippelová 1972 and *potentilletosum anserinae* Krippelová 1972. Besides she recognized within this association the stadium of *Polygonum aviculare* (comparable to the *Matricario-Polygonetum typicum* described by Oberdorfer 1971) and the stadium of *Plantago major*. As *Lolium perenne* occurs with high coverage and high frequency (100%) in the subassociation *typicum* and as species of the *Cynosurion* are almost absent in this community, the unit *Lolio-Plantaginetum* should be maintained. Although *Lolium perenne* occurs with a high presence in communities belonging to the *Cynosurion*, it is obviously a character-species of the *Lolio-Plantaginetum typicum* (KRIPPELOVÁ 1972, KOPECKY 1978).

The assignment of the *Plantaginetalia majoris* to the *Molinio-Arrhenatheretea* can by no means be justified. The same applies for the *Lolio-Potentillion*. This alliance differs considerably in floristic composition from the *Molinio-Arrhenatheretea*. In this class the species *Cynosurus cristatus, Phleum pratense, Plantago lanceolata, Poa pratensis, Festuca rubra, Festuca pratensis, Cerastium fontanum, Ranunculus acris, Trifolium pratense, Rumex acetosa, Holcus lanatus, Vicia cracca, Lathyrus pratensis, Trifolium dubium, Alopecurus pratensis, Arrhenatherum elatius, Bellis perennis, Prunella vulgaris, Leucanthemum vulgare, Veronica chamaedrys* and *Trisetum flavescens* are frequent. On the contrary they are almost absent in the *Lolio-Potentillion*, whereas the opposite applies for a lot of species which are characteristic for this alliance.

As the character-species of the *Plantaginetea, Potentilla anserina, Plantago major, Lolium perenne* and *Poa annua* occur in the *Lolio-Potentillion*, often with high presence degrees in most (*Potentilla anserina, Plantago major*) or in some of the communities (*Lolium perenne* and *Poa annua*), I consider this alliance to belong to this class. Besides the *Lolio-Plantaginetum* and the communities of the *Lolio-Potentillion* are ecologically related by their occurrence on soils which are frequently treaded and are deficient in oxygen. In the *Lolio-Plantaginion* the oxygen deficiency is caused by the compaction of the soil whereas in the *Lolio-Potentillion* it is mainly caused by inundation and waterlogging. Since, on the other hand, the difference in floristic composition and in habitat is obvious, I adopt the opinion of OBERDORFER et al. (1967) to assign the *Lolio-Potentillion* (called *Agropyro-Rumicion* by them) to a separate order, the *Agrostietalia stoloniferae* Oberdorfer, Müller & Görs 1967 (see also GÖRS 1968, MÜLLER & GÖRS 1969). In my opinion the suggested division of the *Lolio-Potentillion* into three suballiances, *Juncion effusi, Loto-Trifolion* and *Eu-Agropyro-Rumicion* (WESTHOFF et al. 1961, WESTHOFF & VAN LEEUWEN 1962, 1966, WESTHOFF & DEN HELD 1969) does not apply for the atlantic domain of Europe.

The *Lolio-Potentillion* occurs in almost all countries of Europe. It is found in the southern part of Sweden, but its northern limitation is still unclear. In the Mediterranean region it is replaced by the vicariant alliance *Trifolio-Cynodontion* Braun-Blanquet & Bolos 1957, which is found under similar ecological conditions, e.g. moist soils poor in oxygen, inundated in winter, grazed by cat-

Fig. 2. The Lolio-Potentillion is restricted to the low-lying inundated zone (January 1980) in a pasture on the bank of a former creek. During summer the water table will be below the soil surface. Just outside the fence where grazing pressure is absent the vegetation is dominated by Phragmites australis.

Fig. 3. The Agrostio-Trifolietum fragiferi inundated by slightly brackish water on an upper salt marsh in The Netherlands (February 1980). The little hummocks are caused by poaching. The little bushes on the small dunes consist of Ononis spinosa and Salix repens.

tle and often poached. In arid or semi-arid climates it is restricted to places where the ground-water level is constantly very high e.g. along rivers with low banks and on frequently inundated islands. It is therefore rather rare and occupies only small areas. The *Caricetum divisae*, subassociation of *Leucojum aestivum* and *Galium constrictum* as described by DONKER & STEVELINK 1961, should be assigned to the *Trifolio-Cynodontion* (BRAUN-BLANQUET & BOLOS 1957, TÜXEN & OBERDORFER 1958, BOLOS 1967, RIVAS-MARTINEZ 1968, BOLOS et al. 1970). J. TÜXEN (1966) is of the opinion that the floristic differences between these two alliances is insufficient and he therefore proposes to abandon the alliance *Trifolio-Cynodontion*. As this alliance has been studied insufficiently no definite enunciation can be made.

Synecology: The communities belonging to the *Lolio-Potentillion* are mainly composed of reptant hemicryptophytes and rhizome-geophytes. These plants have a capacity for rapid vegetative spread and are efficient colonizers of temporary gaps. They occur in water meadows, river forelands, along former river beds, beside pools resulting from dike bursts, in or along depressions containing stagnant water, at the edge of drinking pools for cattle, along ditches, on higher salt marshes and along former creeks, now surrounded by polders. They are found on all kinds of relatively nutrient-rich, hydromorphic soils, varying from sand to heavy clay soils and soils with a peaty top soil layer of about 10 cm consisting for almost 100% of organic material. Most of the species characterizing this alliance have their optimal occurrence on soils moderately rich to rich in nitrogen (ELLENBERG 1978). A mean C/N ratio of 13 ($n = 16$, $\sigma = 2$) measured in the *Ranunculo- Alopecuretum*, the *Nasturtio-Alopecuretum* and the *Agrostio-Trifolietum fragiferi* indicates a rather rapid mineralization. The main factors associated with their occurrence are winter and spring inundation (often with silt or sand deposition) and grazing. The composing species belong to the trichohygrophyta (HEJNY 1960); germination, flowering and maturation of the seed take place in the terrestrial phase when the soil is still moist. A long limose phase offers favourable conditions and a secondary flooding is tolerated.

The flooding (*figs. 2* and *3*) leads to oxygen depletion of the soil which again causes the formation of Mn^{++}-ions, Fe^{++}-ions and reduction of sulphate into sulphides. CO_2, organic acids and for instance methane are produced by decomposition of organic material (BRÜMMER 1974). While lack of oxygen can seriously trouble the respiration in the cell, the substances mentioned above are toxic to many species. Under anaerobic conditions phosphorus is easily available (SCHEFFER et al. 1976). This is in concordance with the fact that most of the species characteristic for the *Lolio-Potentillion* have their highest relative average frequencies on soils with a rather high (P-citric acid 51–80) to high (P-citric acid > 80) phospor status (KRUYNE et al. 1967). Flood sensitive species appear to be excluded from frequently flooded habitats due to the production of increased amounts of ethanol resulting from an increased rate of glycolysis induced by the anaerobic conditions. This accumulation of toxic quantities of

ethanol does not occur in flood-tolerant species. According to some evidence a metabolic switch in the latter species may lead to the accumulation of mainly the non-toxic malic acid (HENSHAW et al. 1962, CRAWFORD & MC MANNON 1968, CRAWFORD & TYLER 1969, CRAWFORD 1966, CRAWFORD 1969, MC MANNON & CRAWFORD 1971).

Various plant species avoid oxygen stress by means of oxygen diffusion through stems, rhizomes and roots. *Lolio-Potentillion* species possessing aerenchymous tissues in stem and roots are for instance *Alopecurus geniculatus, Inula britannica, Agrostis stolonifera* and *Potentilla anserina* (WALTHER 1977). Radial oxygen loss from the roots of these plants is of considerable benefit to wetland species as it oxydises the reduced soil toxins (CONWAY 1940, ARMSTRONG 1964, 1967, 1971; BRÄNDLE 1980a, b). Of course this oxygen transport is only possible if the plants are partly emerged. As plant activity is stimulated by higher temperatures, inundation during the summer season is of more influence than winter inundation. According to KLAPP (1971) in a temperate climate growth of grassland species starts at 5°C and abundant growth only above 10°C. By growing on frequently inundated sites, the *Lolio-Potentillion* species avoid competition from flood-sensitive grassland species (DIERSCHKE & JECKEL 1980). Species selection is probably already taking place in the seed bank. Most seeds will not normally germinate if the oxygen tension is decreased below that in the atmosphere and after some time their viability becomes impaired (MAYER & POLJAKOFF-MAYBER 1963). Other species can only germinate if the seeds are shed in a very moist habitat. In years of excessive rainfall and flooding a marked general reduction of the abundance and cover of species which cannot survive prolonged inundation periods (e.g. numerous species of the *Molinio-Arrhenatheretea*) can be observed (STOFFERS & KNAPP 1962, KLAPP 1965, BALATOVA-TULAČKOVA 1972, WALTHER 1977). The fluctuations resulting from climatological differences from year to year (ecotypic oscillations) were called "Harmonika-Sukzession" by TÜXEN (1950). For the species in question the flooding (in some communities even with sea water) is a perturbation i.e. a significant deviation from the nominal state (the normal operating range). For the grassland species sensitive to flooding, the oxygen depletion induced by the inundation is a severe unfavourable deflection or stress (sensu ODUM et al. 1979). In the *Lolio-Potentillion* the fluctuation in the hydrology does not act as a stress but as a subsidy i.e. it improves the performance of the ecosystem. The elimination of these natural pulses will severely perturb the "perturbation-dependent" ecosystem (VAN LEEUWEN 1958, VAN LEEUWEN & WESTHOFF 1961, WESTHOFF et al. 1961, WESTHOFF & VAN LEEUWEN 1966, BAKKER 1965).

The species composing the *Lolio-Potentillion* belong to the category of ruderal-perennial herbs (GRIME 1979). Ruderals sensu Grime are species that thrive under conditions of low stress (sensu Grime) and high disturbance. Grime has unfortunately broadened the concept ruderal. It is used in botanical literature for species growing on rubble (latin: rudus) and disturbed road sides, e.g. *Sisymbrion* and *Onopordietalia* (ELLENBERG 1978, WILMANNS 1978). The communities to which they belong are strongly influenced by man. The term ruder-

al sensu Grime also comprises communities where disturbances have a natural cause as for instance flooding in the case of the *Lolio-Potentillion*. The anthropogenic influence here is grazing but as will be stated further down, this alliance can also occur under conditions of natural grazing. By preventing the establishment of tall growing species, grazing is advantageous to the low creeping hemicryptophytes and rhizome-geophytes (KLAPP 1971).

Although deep and often numerous hoofprints are seldom absent, poaching is not a necessary condition for the development of the *Lolio-Potentillion*. Totally untrampled but short-grazed sites often occur immediately outside the pasture fence bearing excellently developed *Lolio-Potentillion*. In ELLENBERG 1978 an outline is given of the influence of trampling on the vegetation (see also KLAPP 1971). Soil compaction resulting from this phenomenon again reduces the aeration of the soil.

As grazing by wild herbivores and frequent inundation along uncontrolled rivers were common in the European lowland, this alliance must have existed in prehistoric times (LOHMEYER 1954, WESTHOFF & VAN LEEUWEN 1966, GROENMAN-VAN WAATERINGE 1968, KLAPP 1971, Anonymous 1979). Nowadays human pressure has increased so severely that this alliance although very characteristic for the North European lowland, is declining in a considerable way (FRILEUX 1976, DIERSCHKE 1978, DIERSCHKE & JECKEL 1980). The main factor involved in this process is the drastic land drainage and the consequent lowering of the water tables. Wetlands present the most obvious of challenges to the farmer intent on agricultural intensification (SMEETS et al. 1980). Anything that is wet can be drained – at a price (SHOARD 1980).

In Europe in general the last two decades have witnessed a very impressive increase in field drainage to such an extent that it now is one of the leading factors in rural environmental change (GREEN 1980). Besides drainage the intensive use of herbicides, the large scale use of inorganic fertilizers. overgrazing and an increase in salt influence (MEULEMAN & JOANKNECHT 1980) are detrimental to the *Lolio-Potentillion*.

3.1.1. The lower units

I *Ranunculo-Alopecuretum geniculati* Tüxen 1937.

Synonym: *Rumici-Alopecuretum geniculati* Tüxen 1950.

Syntaxonomy (*table 1* and *2*, clusters nr. 1–11):

Character-species: *Potentilla reptans, Carex hirta, Rorippa sylvestris, Juncus compressus, Inula britannica* and *Mentha pulegium*.

Differential species: *Phalaris arundinacea, Polygonum amphibium, Taraxacum officinale* group, *Elymus repens, Lysimachia nummularia, Myosotis scorpioides, Rorippa amphibia, Alopecurus pratensis, Equisetum palustre, Glechoma hederacea* and *Glyceria maxima*.

Constant companion: *Ranunculus repens*.

Inula britannica and *Mentha pulegium* respectively, are rather rare and very rare in The Netherlands (VAN DER MAAREL 1971a, ARNOLDS et al. 1976). *Mentha pulegium* reaches its north-western boundary in Ireland, South England

Cluster number	1	2	3	4	5	6	7	8	9	10	11
Plantaginetea and Lolio-Potentillion											
Agrostis stolonifera	V	IV	IV	V	V	V	V	V	V	V	V
Rumex crispus	V	V	V	V	III	V	V	IV	IV	III	III
Plantago major	II	V	IV	III	IV	V	III	V	IV	II	III
Poa annua	II	III	IV	II	I	I	III	III	I	I	II
c.c.Poa trivialis	I	V	IV	III	V	V	V	V	V	V	V
c.c.Ranunculus repens	I	V	IV	IV	IV	V	V	V	V	V	V
Alopecurus geniculatus		II	V	V	IV	V	III	II	V	IV	V
Rorippetosum sylvestris											
Rorippa sylvestris	IV	IV	V	II	V	IV	I		II		I
Elymus repens	V	V	V	V	V	IV	III	II	II	I	III
Potentilla reptans	III	IV	V	IV	V	II	II	III	I		I
Equisetosum palustris											
Equisetum palustre						II	IV	III	I	IV	II
Trifolium repens	II	III	II	II	I	III	IV	V	IV	IV	IV
Cardamine pratensis						I	II		III	III	II
Equisetum fluviatile						I	I	II	I	III	
Variants + subvariants											
Potentilla anserina	IV	II	IV	IV	II	IV	III	III	III	I	II
Cirsium arvense	III	V	I	II	IV	II	III	III	II	I	I
Phalaris arundinacea	IV	V	IV	II	II	V	IV	III	III	I	I
Polygonum amphibium	II	III	III	I		IV	IV	IV	IV		
Glechoma hederacea		II				II	II	III	I		
Mentha aquatica		I		I		I	II	IV	III	I	I
Carex hirta	I	I	II	IV	V	II	IV	III	III	II	III
Myosotis scorpioides		I	I	II	V	II	III	IV	V	III	I
Holcus lanatus							I		I	V	V
Artemisia vulgaris	II										
Taraxacum officinale gr.	II	V	III	II	I	III	II	III	II	I	III
Alopecurus pratensis	I	IV	I	II		II	II		I		I
Juncus compressus			I	II	IV	I	II	II	I		I
Mentha pulegium					IV						
Calliergonella cuspidata		I	I		IV	I	I		I	I	
Lolium perenne	I	I	I	III	II	II	I	V	II	I	III
Lysimachia nummularia		II	I	I			III	V	III	I	
Bellis perennis		I	I	I				V	I	II	I
Festuca pratensis		II		II		II	II	V	I	III	II
Prunella vulgaris							I	III			
Cerastium fontanum					I		I	III	I	I	I
Glyceria maxima						I	I	III	IV	IV	I
Juncus articulatus			I	I	III	I	I	IV	IV	IV	II
Glyceria fluitans			I			I	I		IV	V	IV
Galium palustre			I	I	I	I	II	II	IV	II	
Remaining species											
Eleocharis palustris		I	II	I	III	II	III	II	III	II	II
Veronica catenata		I	I	II	III	II	I	II	II	I	I
Poa pratensis	II	I	I	II	III	I	I	III	I		
Rorippa amphibia		I	II	I	II	III	II	II	I		
Leontodon autumnalis	III	I	II	I		I	I	III	II		I
Equisetum arvense	III	I	I	III	I		I		I		
Polygonum aviculare	I	I	II	II	I	II	I		I	I	
Stellaria media		I			III	II	I		I		
Juncus bufonius gr.				I	II	I	I	II	II	II	I
Plantago lanceolata		I	I	I	I	I		II	I	I	
Polygonum hydropiper		I	I	I		I	I	II	I	I	I
Ranunculus sceleratus			I	I	II	I	I		I	I	
Myosotis laxa ssp.caespitosa			I			I	I	II	I	I	I
Oenanthe aquatica		I		I		I	I	II	I		I
Rumex obtusifolius	II	II	I			II			I		I
Trifolium fragiferum					I	I	I		II		I
Urtica dioica		II	I			I	I		I		
Trifolium pratense			I					II	I		I
Mentha arvensis				II		I	I		I		
Phleum pratense				I		I		II	II		
Iris pseudacorus		II				I	I		I		
Veronica serpyllifolia							I	II	I		I
Butomus umbellatus			II			I	I			I	
Oenanthe fistulosa								II	II	I	
Ranunculus acris							I	II			I
Rumex conglomeratus			I	I			I	II	II		
Carex otrubae						I	I	II	I		
Juncus inflexus						I	I	II	I		
Lychnis flos-cuculi						I		II			

and The Netherlands. In The Netherlands it has been recorded only in nine hoursquares since 1950. A new locality has been found in 1981 (ADEMA 1981). Its decline from 47 hoursquares before 1950 is probably due to a change in water control (ADEMA 1980). In the literature (WESTHOFF & DEN HELD 1969, OBERDORFER 1970, VICHEREK 1973, KNEEPKENS & VERHOEVEN 1975, ELLENBERG 1978) these species are considered to be character-species of the *Lolio-Potentillion* (*Agropyro-Rumicion crispi* sensu Tüxen 1950); in *table 1* they are represented in the *Ranunculo-Alopecuretum* only, so that they are considered to be characteristic for this association.

Elymus repens and *Ranunculus repens* are neither character-species of the alliance nor of the *Ranunculo-Alopercuretum*. *Elymus repens* has a wide ecological amplitude and occurs with presence class IV or V in several communities (see *table 3*). These communities occur on arable lands, recently disturbed soils, ruderal and otherwise anthropogenically influenced sites.

According to PALMER & SAGAR (1963) *Elymus repens* is usually found in waste places and on arable land where tree or shrub cover is not continuous. It is a common component of lightly grazed grassland communities of basic soils in Britain, a pioneer plant in the colonization of waste places, a pest of agriculture, especially associated with arable land. In case of disturbance of the vegetation cover this species is quickly colonizing the gaps by means of its prolific vegetative reproduction through rhizomes (PALMER & SAGAR 1963). *Elymus repens* is both very resistant against drought and against flooding (KRUYNE & DE VRIES 1968). It has been observed to spread impressively as a reaction to overfertilization with nitrogen (LAMBERT 1979). MÜLLER & GÖRS (1969) consider it to be a character-species of the *Convolvulo-Agropyrion repentis* Görs 1966, *Agropyretea intermedii-repentis* Oberdorfer, Müller & Görs 1967, semi ruderal grasslands from dry and medium dry sites. Originally, before the creation of these antrhopogenic habitats, the optimal occurrence of *Elymus repens* must have been in natural *Lolio-Potentillion* communities where open places were created by the influence of inundation (e.g. sedimentation, erosion) or poaching.

Ranunculus repens occurs with high presence class in some *Magnocaricion*-communities, especially in the *Phalaridetum arundinaceae* Libb. 1931 and the *Caricetum gracilis* (Graebn. & Hueck 1931) Tüxen 1937 as well as in several communities of the *Calthion palustris* Tüxen 1937 em. 1951, especially in the *Cirsietum oleracei* Tüxen (1937) 1951 and the *Juncetum subnodulosi* Koch 1936 (PASSARGE 1964). It is a weed of grassland and arable land and of recently disturbed ground. *Ranunculus repens* is especially abundant where drainage is impeded and is found mainly on heavy wet soils. Colonization of open ground is quickly effected by the production of long stolons (HARPER 1957). These conditions explain its high presence in the *Lolio-Potentillion*.

a) Subassociation *typicum* (cluster nr. 6). This subassociation takes a central position between the other subassociations.
b) Subassociation *rorippetosum sylvestris* (clusters nr. 1–5). Differential spe-

Table 3. Communities in which Elymus repens is found with presence class IV or V (PASSARGE 1964, WESTHOFF & DEN HELD 1969, KOPECKÝ 1978, RUNGE 1980).

I Polygono-Chenopodion W. Koch 1926 em. Sissingh 1946 denuo em. Oberd. 1957.
  1. Chrysanthemo-Sperguletum (Br.-Bl. & De Leeuw 1936) Tx. 1937
  2. Chenopodietum albi Pass. 1955
  3. Digitarietum ischaemi Tx. & Prsg. (1942) 1950
  4. Lycopsetum arvensis Raabe 1944
  5. Mercuriali-Fumarietum (Kruseman & Vl. 1939) em. Tx. 1950
  6. Veronico-Lamietum hybridi Kruseman & Vl. 1939
II Sisymbrion Tx., Lohm. & Prsg. 1940
  1. Agropyro-Convolvuletum arvensis Feldföldy 1943
III Arction (Tx. 1937) em. Sissingh 1946
  1. Lamio-Conietum Oberdorfer 1957
  2. Artemisietum vulgaris (Br.-Bl. '31) Tx. 1942
IV Aegopodion podagrariae Tx. 1967
  1. Aegopodietum Tx. 1967
V Trifolion medii Th. Müller 1961
  1. Urtico-Cruciatetum laevipes Dierschke 1973
VI Derivate community of [Agropyron repens-Arrhenatheretalia] Kopecký 1978.

cies: *Rorippa sylvestris, Elymus repens* and *Potentilla reptans.*
Variant with *Phalaris arundinacea* and *Polygonum amphibium* (clusters nr. 1–3).
Variant with *Carex hirta* and *Myosotis scorpioides* (clusters nr. 4 & 5).
c) Subassociation *equisetetosum palustris* (clusters nr. 7–11). Differential species: *Equisetum palustre, Trifolium repens, Cardamine pratensis* and *Equisetum fluviatile.*
Variant with *Polygonum amphibium* and *Phalaris arundinacea,* (clusters nr. 7–9).
Variant with *Holcus lanatus* (clusters nr. 10 & 11).
Within the *Ranunculo-Alopecuretum* each cluster represents a unit below the variant. These units will not be discussed here. The differential species are apparent from *table 2.*
Synecology: The subassociation *rorippetosum sylvestris* is confined to sites with a low ground water table and a dry top soil after the retreat of the water. The water table is often situated more than one meter below the ground level. This subassociation is found on sandy ridges and sandy river shores (cluster 1), in pastures in the river forelands mainly on heavy clay and sometimes on sandy clay. In summer the clay becomes very hard and fissured by desiccation. It also occurs on steep banks along pools resulting from former dike bursts and on the foot of dikes with only five to ten centimeter of soil (clay, sometimes sand) on a stoney or asphalt underground.

The two variants mainly result from a difference in grazing intensity. The variant with *Phalaris arundinacea* is mainly found in alternate pastures and in hay pastures. This is in concordance with the results of KRUYNE et al. (1967), which demonstrate that *Phalaris arundinacea* and *Polygonum amphibium* have their highest relative average frequencies in pure hayfields and hay pastures

and the lowest in alternate pastures and pure pastures.

The variant with *Carex hirta* and *Myosotis scorpioides* on the contrary is found in pure pastures. Concerning *Carex hirta* this is again in concordance with the data from KRUYNE et al. 1967. *Myosotis scorpioides* on the other hand has a highest relative average frequency in hay pastures. In this case it is confined to the variant with *Carex hirta* and *Myosotis scorpioides,* a community from pastures with a slightly higher water table and a somewhat moister top soil.

In the subassociation *equisetetosum palustris* the water table is a long time above the surface and close to the soil surface even in the driest period. In almost all cases it has been found adjacent to open water, along former river beds, pools resulting from dike bursts, marshy, severely poached ditch banks, on the bottom of ditches and drainage furrows. Measurements revealed that the ground-water level was always within 30 cm from the soil surface, in many cases at the same level as, or even sometimes $\pm$ 5 cm above the soil surface. The *Ranunculo-Alopecuretum geniculati equisetetosum palustris* occurs on heavy clay, sandy clay and peaty soils. Because of the high water content these soils are very soft resulting in the presence of many, often deep hoofprints.

The variant with *Phalaris arundinacea* and *Polygonum amphibium,* is almost restricted to the river forelands where the hydrological dynamics are more pronounced than in the sites where the variant of *Holcus lanatus* is found. While the former variant is yearly inundated by a deep water layer, the depth of the water in the latter is always restricted to about 20 cm, permitting species like *Holcus lanatus* to be emerged during the greater part of the growing season. The variant with *Holcus lanatus* was not found in river forelands but in moist pastures mostly in the polder areas, mainly on peaty soils, on soils consisting of 5–10 cm of organic material on clay or sand, on sandy clay and on clay.

The subassociation *typicum* is intermediate in its hydrological characteristics. It occurs in river forelands, mainly on heavy clay, sandy clay and sometimes on sand.

II Association group with *Eleocharis uniglumis.*
Syntaxonomy:
Character-species: *Eleocharis uniglumis.*
Differential species: *Phragmites australis, Festuca arundinacea.*
These three taxa combine the three associations:
Nasturtio-Alopecuretum geniculati
Triglochino-Agrostietum stoloniferae
Agrostio-Trifolietum fragiferi.
Synecology: The associations belonging to this group are restricted to habitats where the top soil never desiccates. The hydrology is considerably less dynamical than in the river forelands.

A. *Nasturtio-Alopecuretum geniculati* ass.nov.
Syntaxonomy (*table 1*):

Local character-species: *Ranunculus sardous*.
Differential species: *Nasturtium microphyllum, Ranunculus sceleratus, Veronica catenata, Epilobium parviflorum.*
Constant companions: *Ranunculus repens* and *Glyceria fluitans.*
Nomenclatural type:
Locality: Zeeuws Vlaanderen, "Cambronkreek", a former creek;
Date: 15th of June 1978;
Size: 5 m^2; Total cover 95%; height 20–50 cm; soil type: sandy clay.
Ranunculus sardous +, *Nasturtium microphyllum* 1, *Ranunculus sceleratus* +, *Veronica catenata* +, *Epilobium parviflorum* +, *Ranunculus repens* +, *Glyceria declinata* 1, *Alopecurus geniculatus* 2a, *Rumex crispus* 3, *Agrostis stolonifera* 5, *Juncus articulatus* +, *Eleocharis uniglumis* 1, *Poa trivialis* 2a, *Festuca arundinacea* +, *Trifolium fragiferum* +, *Phragmites australis* +, *Scirpus lacustris* ssp. *tabernaemontani* 1, *Phalaris arundinacea* +, *Oenanthe aquatica* +, *Mentha aquatica* 2, *Brachythecium rutabulum* +.

Relevés of this community have also been made by me in Belgium, N.W. France, Britain and Ireland. The *Nasturtio-Alopecuretum* is transitional to the *Helosciadetum nodiflori* Braun-Blanquet 1931 and the *Nasturtietum officinalis* Seib. 1962 (*Glycerio-Sparganion* Braun-Blanquet et Sissingh 1942). It is often adjoined by these communities and by the *Bidention* Nordhagen 1940. Although *Apium nodiflorum* rarely occurs in the Dutch material, it is regularly found in the relevés made abroad. This species reaches its northern limit in The Netherlands and is rather rare (TUTIN et al. 1968, ARNOLDS et al. 1975).
Synecology: The association occurs along ditches and along former creeks now lying inland. The very soft, severely poached sandy clay soils are water saturated throughout the year. The top soil consists of slime mixed with organic material. The water level is situated at 10–20 cm above the soil surface during the greater part of the year. The presence of shells in the soil indicates a high calcium content.

B. *Triglochino-Agrostietum stoloniferae* Konczak 1968.
Syntaxonomy (*tables 1* and *4*):
Character-species: *Triglochin palustris.*
Differential species: *Juncus articulatus, Galium palustre, Ranunculus flammula, Hydrocotyle vulgaris, Carex nigra, Myosotis laxa* spp. *caespitosa.* Lectotype: relevé nr. 5, table 18 from KONCKZAK 1968. The table given by Konczak (1968) is somewhat complex and the floristic composition of this table is not sufficiently characteristic for this association. This is probably caused by the fact that his relevés are made on relatively dry sites (water table at a depth of 60 cm on 20-8-1964) and originate from a restricted locality, viz. the Havelseen near Potsdam. *Triglochin palustris* has been considered a character-species of the *Scheuchzerio-Caricetea fuscae* Nordhagen 1939 (KRAUSCH 1968, OBERDORFER 1970 and 1977, ELLENBERG 1978). Close examination of published synoptic tables shows that this does not apply. It is absent in most of the communities belonging to that class, while in the other communities its presence class does

	cluster number				
	18	19	20	21	22
Agrostis stolonifera	V	V	V	V	IV
Potentilla anserina	V	III	V	V	V
Eleocharis uniglumis	II	II	IV	III	III
Juncus articulatus	IV	V	V	V	V
Galium palustre	IV	V	V	IV	II
Alopecurus geniculatus	III	V	IV	I	II
Ranunculus flammula	IV	III	V	III	V
Hydrocotyle vulgaris	IV	III	V	V	II
Carex nigra	V		V	V	V
Ranunculetosum repentis and Juncetosum gerardii					
c.c.Poa trivialis	I	V	III	I	IV
Phragmites australis	I	III	V	IV	III
Triglochin palustris		V	III	II	IV
Ranunculetosum repentis					
Ranunculus repens	II	V	V	II	
Lolium perenne		III	II		
Juncetosum gerardii					
Juncus gerardi	I	II	I	V	V
Glaux maritima	I			IV	V
Inops					
Stellaria palustris	II				
Carex panicea	II				
Variants					
Cardamine pratensis	II	V	IV	III	
Juncus bufonius group	II	I	II	III	
Mentha aquatica	I	IV	III	II	
Leontodon autumnalis	II	III	IV	III	I
Myosotis laxa ssp.caespitosa	I	IV	V	III	
Plantago major	I	IV	I	II	
Holcus lanatus	II	IV		I	I
Scirpus lacustris ssp tabernaemontani		IV			
Festuca arundinacea		III			
Senecio aquaticus		III			
Berula erecta		III			
Lysimachia nummularia		II			
Epilobium palustre		II			
Eleocharis palustris			V		
Rumex crispus	I	I	III		
Carex disticha			III		
Plantago lanceolata			II		
Vicia cracca			II		
Calliergonella cuspidata				IV	
Carex serotina				II	
Anagallis minima				II	
Centaurium pulchellum				II	
Trifolium fragiferum					V
Eleocharis quinqueflora					IV
Brachythecium rutabulum					IV
Remaining species					
Trifolium repens	II	IV	II	II	IV
Glyceria fluitans	I	III	II		
Polygonum amphibium	I	I	II		
Ranunculus sceleratus		II		I	
Triglochin maritima		I		I	II
Lotus corniculatus	II	II		I	
Poa pratensis	I		II	I	I
Cerastium fontanum		II	I		
Mentha arvensis	II		I		III
Equisetum arvensis			II	I	
Sagina procumbens	I	III		III	
Lycopus europaeus	II	I	II	I	
Veronica scutellata	II		I	I	
Juncus effusus	II	II			
Drepanocladus aduncus	I	II	II	I	II

not exceed II (PASSARGE 1964, KRAUSCH 1968, OBERDORFER 1977, ZIJLSTRA 1981). In TÜXEN (1937) *Triglochin palustris* is absent from the *Scheuchzerietalia,* but occurs in the *Ranunculus repens-Alopecurus geniculatus* association, subassociation of *Eleocharis uniglumis* Tüxen et Hintz 1937, with presence class IV.

In agreement with VAN OOSTSTROOM (1954) I consider the species to have its optimal occurrence in the *Lolio-Potentillion* (*Agropyro-Rumicion crispi* Tüxen 1950 p.p.) and more in particular as a character-species of the *Triglochino-Agrostietum stoloniferae* (compare *table 1*).

a) Subassociation *ranunculetosum repentis* (19–20)
   Differential species: *Ranunculus repens, Lolium perenne.*
b) Subassociation *Juncetosum gerardii*
   Differential species: *Juncus gerardi, Glaux maritima.*
c) Subassociation *inops*: This species-poor community is characterized by the absence of differential species.

Synecology: The *Triglochino-Agrostietum stoloniferae* is restricted to pastures without any artificial manuring. Consequently the nutrient status is low and the soil is moderately acid. The character- and differential species have their highest presence on wet, moderately to strongly acid, peaty to pure peat soils, with a rather low to low (P-citric acid 0–20 and 21–32 respectively) phosphorus status (KRUYNE et al. 1967, KRUYNE & DE VRIES 1968); their optimal occurrence is on soils which are poor to very poor in nitrogen (ELLENBERG 1978). Throughout the year the water table stands just above or just beneath the soil surface.

The association has an affinity to the *Caricion curto-nigrae* W. Koch 1926 em. Nordhagen 1936, the small sedge communities, peat building, mesotraphent communities from calcium-poor soils (WESTHOFF et al. 1969, OBERDORFER 1977). In The Netherlands these communities as well as the *Triglochino-Agrostietum* are very rare at present, because of the extensive use of artificial fertilizers, often in combination with drainage.

The subassociation *ranunculetosum repentis* is confined to marshy fresh soils. It has been found in and along ditches, along former creeks in a pasture grazed by pigs, along dune slacks and in a ditch shaded by *Pinus sylvestris.* The soil consists of brown peaty clay, peat, clay, sandy clay or sand rich in organic material.

The subassociation *juncetosum gerardii* occurs under slightly brackish conditions. Two samples taken from water inundating this community on the 27th of February, each contained $0.46^0/_{00}$ Cl^-. It occurs on the higher saltmarshes where it is inundated with seawater during high water spring tides, but only when there is a considerable influence of fresh water from lateral seepage out of surrounding dunes or from stagnant rain water. It is also found on saltmarshes nowadays inaccessible for the sea where the salt has partly been washed out of the soil. The top soil (5–10 cm) consists of peat, sometimes mixed with sand, on grey, reduced sand. Compared to the situation in the other subassociations, the top soil of the subassociation *inops* is drier in summer. In some

	cluster number			
	23	24	25	26
Agrostis stolonifera	V	V	V	V
Potentilla anserina	V	II	V	V
Juncus gerardi	V	V	V	V
Glaux maritima	IV	V	II	V
Eleocharis uniglumis	IV	V	I	III
C.c. Trifolium repens	II	IV	V	V
Typicum, festucetosum rubrae and Onondo-Caricetum.				
Carex distans		IV	IV	IV
Leontodon autumnalis		III	III	III
Triglochin maritima		II	II	I
Typicum and festucetosum rubrae				
Trifolium fragiferum	I	V	III	II
Centaurium pulchellum	I	V	III	
Typicum				
Plantago major	II	IV	II	
Phragmites australis	II	IV	II	II
Drepanocladus aduncus		IV		
Poa trivialis	I	III	I	
Carex otrubae	I	III		
Samolus valerandi		III		
Lotus tenuis		III	I	
Bellis perennis		III		
Festucetosum rubrae and Onondo-Caricetum				
Festuca rubra	I		V	V
Holcus lanatus	I	I	V	V
Poa pratensis	I	I	IV	V
Plantago coronopus	I	I	III	III
Odontites verna ssp serotina	II		III	III
Plantago maritima	I	I	III	III
Centaurium littorale			II	II
Onondo-Caricetum				
Cerastium fontanum			III	V
Ononis spinosa		I	I	V
Armeria maritima			II	IV
Lotus corniculatus			I	IV
Trifolium pratense		I	I	III
Cochlearica danica				II
Elymus pungens				II
Remaining species				
Lolium perenne	I	II	I	
Festuca arundinacea	II	III	II	I
Scirpus maritimus	II	III		
Juncus articulatus	I	III	II	I
Galium palustre	II	I		
Triglochin palustris	I	II	II	
Carex nigra	I		II	I
Cirsium arvense	I		II	I
Juncus bufonius group	I	III	II	I
Sagina procumbens		I	II	II
Alopecurus geniculatus	II			
Scirpus lacustris ssp tabernaemontani	I	II		
Leontodon taraxacoides		I	II	II
Salix repens	I		I	II
Brachythecium rutabulum	II	III	III	III

cases it even runs fully dry, i.e. a layer of dry papery organic material is formed on a moist sandy subsoil.

C. *Agrostio-Trifolietum fragiferi* ass.nov. (cluster nr. 23–25). Synonym: community of *Agrostis stolonifera* subvar. *salina and Trifolium fragiferum* Westhoff 1947.

Syntaxonomy (*tables 1* and *5*):

Character-species: *Trifolium fragiferum.*

Differential species: *Juncus gerardi, Glaux maritima, Carex distans, Centaurium pulchellum.*

Constant companion: *Trifolium repens.*

Nomenclatural type:

Locality: Noord-Beveland.

Date: 27th of July 1978.

Size: 9 m²; total cover 98%; height 10–25 cm; soil type: 5 cm organic material on grey reduced sand.

Agrostis stolonifera 4, *Trifolium repens* 2b, *Trifolium fragiferum* 3, *Festuca arundinacea* 2b, *Carex distans* 2a, *Carex otrubae* +, *Centaurium pulchellum* 1, *Lotus tenuis* +, *Triglochin maritima* +, *Scirpus maritimus* +, *Plantago major* +, *Ononis spinosa* +, *Juncus gerardi* 3, *Phragmites australis* 1, *Bellis perennis* +, *Samolus valerandi* 1, *Juncus articulatus* +, *Poa trivialis* 1, *Lolium perenne* +, *Glaux maritima* 1, *Poa annua* 1, *Leontodon autumnalis* +, *Drepanocladus aduncus* 4, *Brachythecium rutabulum* 1.

a) Subassociation *typicum* (cluster nr. 24).

Differential species: *Plantago major, Phragmites australis, Drepanocladus aduncus, Poa trivialis, Carex otrubae, Samolus valerandi, Lotus tenuis, Bellis perennis.*

Carex otrubae is probably a character-species of the *Agrostio-Trifolietum fragiferi*; in this association it has a high presence in Belgium and France too. Its status will be decided after the interpretation of the relevés made in these countries.

b) Subassociation *festucetosum rubrae* (cluster nr. 25).

Differential species: *Festuca rubra, Holcus lanatus, Poa pratensis, Plantago coronopus, Odontites verna* spp. *serotina, Plantago maritima, Cerastium fontanum, Centaurium litorale.*

The *festucetosum rubrae* is a transition community between the subassociation *typicum* and the *Ononido-Caricetum distantis* Tüxen 1955.

c) Subassociation *inops* (cluster nr. 23). Synonym: *Agrostis stolonifera-Potentilla anserina* community Runge 1966.

This subassociation is negatively characterized by the absence or very low presence of the differential species of the other subassociations and of *Carex distans, Leontodon autumnalis, Triglochin maritima, Trifolium fragiferum* and *Centaurium pulchellum.*

Synecology: The habitats of the subassociations *typicum* and *festucetosum rubrae* differ mainly in salt influence. The subassociation *typicum* has only been

found on slightly brackish soils out of reach of the sea. The *festucetosum rubrae* is inundated irregularly in winter during high water spring tides by sea water. The former occurs on sites adjacent to the inland slopes of sea dikes through which sea water is percolating and on primary dune slacks. The latter is restricted to higher salt marshes (*fig. 3*) and to so called "sluftervlakten" i.e. salt marshes of restricted surface behind the dunes in connection with the sea through a narrow inlet. Three samples taken from water inundating the subassociation *festucetosum rubrae* on the 27th of February 1980 contained 1.23, 1.93 and 2.13 $^0/_{00}$ Cl^- respectively. Both habitats have the same soil composition viz. 5–10 cm of silt rich in organic material, on grey, reduced sand.

The subassociation *inops* experiences very low grazing pressure. On some sites the vegetation was grazed very extensively by sheep, on other sites by cattle and sometimes even by rabbits only. It often occurs as low lying patches surrounded by a stand dominated by *Juncus maritimus, Calamagrostis epigejos, Schoenus nigricans* or *Festuca rubra* (*fig. 4*).

III Other units.

A. *Ononido-Caricetum distantis* Runge 1966. Synonym: *Ononis spinosa-Carex distans* association Tüxen 1955 nomen nudum.

Syntaxonomy (*tables 1* and *5*, cluster nr. 26).

Local character-species: *Ononis spinosa.*

Westhoff & Den Held (1969) assigned this association to the *Agropyro-Rumicion* (*Lolio-Potentillion*). Although it has a strong affinity to the *Agrostio-Trifolietum fragiferi* (*table 5*), the preponderance of *Glauco-Puccinellietalia* and *Armerion* species, like *Plantago maritima, Armeria maritima, Festuca rubra* ssp. *litoralis, Centaurium litorale, Juncus gerardi, Carex distans* and *Glaux maritima,* justifies its classification into the *Armerion,* as has been done by Tüxen (1955) and Runge (1980). The *Ononido-Caricetum* has only been recorded on the Wadden islands and along the coast of the Baltic Sea.

Synecology: The *Ononido-Caricetum distantis* occurs as a zone above the *Agrostio-Trifolietum fragiferi festucetosum rubrae* on small dunes in extensively grazed upper salt marshes. The soil is composed of a top layer of about 5 cm which is very rich in organic material, lying on sand. The colour of the sandy subsoil is yellow indicating that reduction of the soil is considerably less severe than in the grey subsoil of the *Agrostio-Trifolietum.* The association occurs 40–60 cm above mean high tide level (Runge 1980). the vegetation is hardly grazed due to the protection given by the spines of the *Ononis spinosa* bushes.

B. Derivate community (Derivatgesellschaft sensu Kopecký & Hejný 1978) of *Festuca arundinacea-[Lolio-Potentillion].*

Syntaxonomy (*tables 1* and *6*, clusters nr. 12 and 13): This community is characterized by the high presence and high coverage of *Festuca arundinacea.* As character-taxa of lower units are hardly present and as this community has no character-taxon of its own, it can be considered a derivate community of the alliance (Kopecký & Hejný 1974, 1978). Within this community two types

	cluster number 12	13
Festuca arundinacea	V	V
Agrostis stolonifera	V	V
Poa trivialis	IV	V
Rumex crispus	III	IV
Potentilla anserina	III	II
Carex otrubae	II	III
Ranunculus sardous	II	III
Phragmites australis	II	I
Lolium perenne type:		
Lolium perenne	IV	II
Elymus repens	IV	
Ranunculus acris	II	
Urtica dioica	II	
Alopecurus geniculatus type:		
Trifolium repens	III	V
Ranunculus repens	III	V
Plantago major	II	IV
Alopecurus geniculatus	II	IV
Taraxacum officinale group	I	III
Carex hirta		III
Eleocharis uniglumis	I	III
Equisetum palustre		II
Nasturtium microphyllum		II
Eleocharis palustris		II
Glyceria fluitans		II
Remaining species		
Holcus lanatus	III	IV
Bellis perennis	II	III
Cirsium arvense	III	II
Cerastium fontanum	III	II
Rumex conglomeratus	I	II
Scirpus maritimus	I	II
Juncus articulatus	I	II
Trifolium fragiferum	I	II
Mentha aquatica	I	II
Cardamine pratensis	I	II
Brachythecium rutabulum	I	II

can be distinguished:
a) the *Lolium perenne* type is characterized by the presence of *Lolium perenne, Elymus repens,* and, with a lower presence, *Ranunculus acris* and *Urtica dioica.*
b) the *Alopecurus geniculatus* type is characterized by the higher presence of *Trifolium repens, Ranunculus repens, Plantago major, Alopecurus geniculatus, Taraxacum officinale* group, *Carex hirta, Eleocharis uniglumis, Nasturtium microphyllum, Eleocharis palustris* and *Glyceria fluitans.*

As *Festuca arundinacea* can be found with high coverage in all kinds of grasslands under special management conditions, it is neither a character-species of this community nor of the *Potentillo-Festucetum arundinaceae* Tüxen 1950, or of any other community within the *Lolio-Potentillion. Festuca arundinacea* dominated vegetation types are of common occurrence on most of the dikes in The Netherlands. These sites are never inundated, ungrazed, irregularly burned and they contain a heavy clay soil. Under these conditions *Festuca arundinacea* tussocks are accompanied by *Molinio-Arrhenatheretea* species while *Lolio-Potentillion* species are hardly present or altogether absent. This situation can be found both in ruderal forms of *Arrhenatheretum* as well as in irregularly grazed *Lolio-Cynosuretum* communities (SÝKORA & SÝKORA-HENDRIKS 1977, SÝKORA-HENDRIKS & SÝKORA 1973 and many unpublished relevés).

That management (selective irregular grazing) rather than hydrology determines the spreading of *Festuca arundinacea*, can be seen in pastures consisting of both a dike and a piece of river foreland. In the same pasture the facies of this species occurs both in the inundated *Lolio-Potentillion* as well as in the adjoining *Lolio-Cynosuretum*.

Synecology: The D.c. *Festuca arundinacea-[Lolio-Potentillion]* was found in irregularly grazed pastures inundated or waterlogged in winter. *Festuca arundinacea* seems especially favoured by irregular horse grazing, but the community also occurs in pastures irregularly grazed by cattle and sheep (KLAPP 1965, 1971). The community occurs on various soils, e.g. peaty soils, on heavy clay, sandy clay and sand. The habitats of the two types differ in hydrology. The *Lolium perenne* type is restricted to sites which are considerably drier during the growth season than those occupied by the *Alopecurus geniculatus* type.

C. Community of *Scirpus maritimus* and *Alopecurus geniculatus*.

Syntaxonomy (*table 1*, cluster nr. 15): This community is a transition between the *Lolio-Potentillion* and the *Scirpetum maritimi* (W. Christ. 1934) Tüxen 1937. Although *Potentilla anserina, Agrostis stolonifera, Alopecurus geniculatus* and *Eleocharis uniglumis* are still frequent the occurrence of *Scirpus maritimus* with presence class V and *Scirpus lacustris glaucus* (presence class III) indicates its affinity with the *Scirpetum maritimi*.

Synecology: This community was found on low lying parts of pastures where the water remains above soil level for most of the year. It occurs under slightly brackish conditions on peaty soils, sandy clay soils, clay and sand. The *Scirpetum maritimi* is permanently inundated by brackish water with a depth of 5 to maximally 100 cm (WESTHOFF & DEN HELD 1969, OBERDORFER 1977, RUNGE 1980).

D. Basal community (Basalgesellschaft sensu Kopecký & Hejný 1978) of *Agrostis stolonifera-[Lolio-Potentillion]*.

Syntaxonomy (*table 1*, clusters nr, 16, 17): On floristic criteria this community cannot be assigned to one of the associations. Two types can be distinguished. The *Scirpus maritimus-Juncus bufonius* type (nr. 17) is almost exclusively composed of the class and alliance character-species *Potentilla anserina, Agrostis stolonifera* and *Alopecurus geniculatus*. Also *Scirpus maritimus* and *Juncus bufonius* occur in this type (presence class III). The *Trifolium fragiferum-Ranunculus sardous* type (cluster nr. 16) is somewhat less severely disturbed and apart from the class and alliance species mentioned for the *Scirpus maritimus-Juncus bufonius* type, it contains *Plantago major* and *Lolium perenne*. Besides *Poa trivialis, Festuca arundinacea, Ranunculus sardous, Juncus gerardi, Trifolium fragiferum* and *Trifolium repens* also occur (with presence class III or more).

Synecology: The main factor in the development of the basal community is disturbance. In some sites the disturbance was caused by severe treading and overgrazing, the vegetation having a height of only 5 cm and in extreme situations scoring only 30% total coverage. In other localities herbicides were used,

Fig. 4. The Agrostio-Trifolietum fragiferi is often constricted to grazed patches between a hardly grazed vegetation in which Juncus maritimus is the dominant species.

a thick layer of organic material was deposited on the pasture, a grazing regime had just recently been started in a formerly unmanaged grassland, a recently reclaimed soil was in the process of desalination, or a pasture was overfertilized with artificial fertilizers or by the droppings of a colony of seagulls.

E. *Juncus maritimus* dominated communities.
In many cases the *Agrostio-Trifolietum fragiferi* can be found as a mosaic of grazed low lying patches between a vegetation dominated by *Juncus maritimus*. The units 27 and 28 (*table 1*) result from relevés made in this adjoining vegetation in order to study its syntaxonomical position. *Juncus maritimus* has been considered to be a differential species with special affinity to the *Agropyro-Rumicion crispi* Nordhagen 1940 em. Tüxen 1950 (Westhoff et al. 1961, Westhoff & Den Held 1969) and some other authors even considered the species to have its optimum in the alliance (Westhoff & Van Leeuwen 1966, Beeftink 1968). According to Beeftink (1968) on the European Atlantic coast *Juncus maritimus* is only a facultative halophyte, with an optimum in the *Agropyro-Rumicion crispi*.

As can be seen in *table 1* the *Juncus* dominated vegetation adjoining the *Agrostio-Trifolietum fragiferi* clearly belongs to the *Juncetum maritimi* Bilik 1956 (*Armerion maritimae* Braun-Blanquet & De Leeuw (1936) and *Juncus maritimus* is by no means characteristic for any of the *Lolio-Potentillion* communities. Moreover one of the essential factors for the development of the *Lolio-Potentillion* is grazing. This is considerably restricted or even prevented be-

tween the coarse *Juncus* bushes. Only on the lower-lying patches where the vegetation is kept short by a sufficiently high grazing pressure, the *Agrostio-Trifolietum fragiferi* is optimally developed (*fig. 4*). The boundary between the two vegetation types is very sharp, forming a convergent limit: limes convergens or ecotone (VAN LEEUWEN 1966, BECKING 1968, VAN DER MAAREL 1971b, SHIMWELL 1971).

F. *Alopecurus arundinaceus* community.
The syntaxonomic position of this community still remains unclear. It has been compared to an *Alopecurus geniculatus* community by TYLER (1969). The absence of a sufficiently strong grazing pressure enables the development of tall *Alopecurus arundinaceus* and *Festuca arundinacea* clumps, thus leading to a more or less ruderal tall forb community. The relevés presented in *table 1* were made near the Baltic Sea on an upper salt marsh. The soil respectively consisted of an upper layer of organic material, litter and even a decaying faggot on a sandy soil. The *Alopecurus arundinaceus* community (see also NORDHAGEN 1954) can certainly not be assigned to the *Lolio-Potentillion*.

3.2. Principal components analysis (*fig. 5*)
Fig. 5 is the result of the ordination of the units represented in *table 1*. The first two dimensions (percentage extracted variance respectively 28 and 12%) illustrate the relations of the units to one another and to the two main environmen-

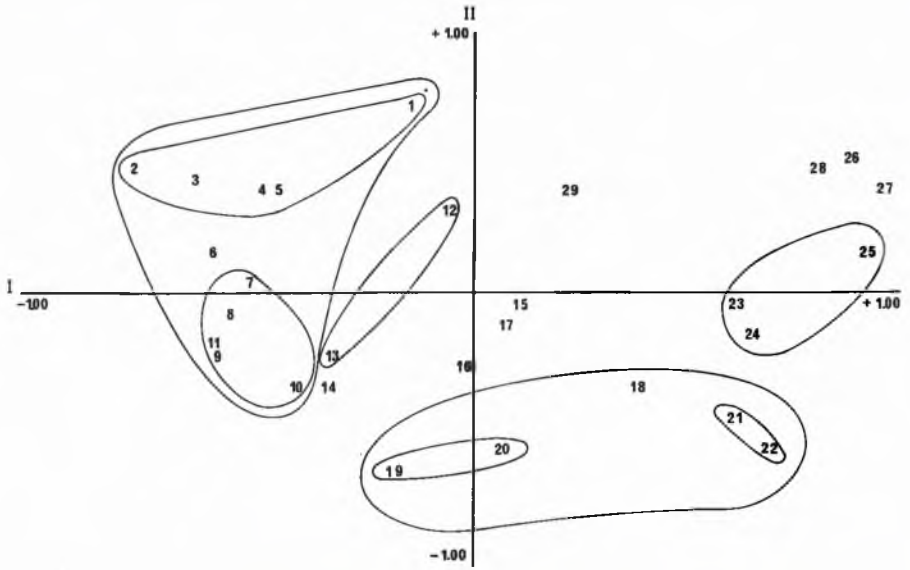


Fig. 5. Ordination of the clusters presented in *table 1*. The numbers used in this figure correspond with the cluster numbers in *table 1*. Dimension 1 corresponds with the salt influence, dimension 2 with the depth of the water table during the growth season. For explanation of the numbers see text and *table 1*.

tal factors. Ecological interpretation of dimension 3 and 4 appeared to give difficulties. Dimension 1 corresponds with an increase in salt influence. The *Ranunculo-Alopecuretum geniculati* (clusters 1–11), the *Nasturtio-Alopecuretum geniculati* (cluster 14) and the derivate community of *Festuca arundinacea-[Lolio-Potentillion]* (cluster 12–13) on the left side of the diagram, are restricted to fresh soils. The *Agrostio-Trifolietum fragiferi* (cluster 23–25), *Juncetum maritimi* (clusters 27–28) and *Ononido-Caricetum distantis* (cluster 26) on the right side are restricted to brackish sites, whereas the community of *Scirpus maritimus* (cluster 15) and the *Alopecurus arundinaceus* community (cluster 29) take an intermediate position.

From the *Triglochino-Agrostietum* the subassociation *ranunculetosum repentis* (clusters 19-20), growing on fresh soils, is found on the left hand side, whereas the subassociation *juncetosum gerardii* (clusters 21–22) from brackish sites occurs in the right hand side of the diagram.

Because the basal community of *Agrostis stolonifera-[Lolio-Potentillion]* (clusters 16–17) and the *Triglochino-Agrostietum inops* (cluster 18) are very poor in species as well as poor in indicative species, their position in the diagram does not clearly show their relation to the salt influence.

The second dimension corresponds with the depth of the water table during the growth season and consequently the extent to which the top soil is desiccating. Within the *Ranunculo-Alopecuretum* the *rorippetosum sylvestris* (clusters 1–5), growing on sites with a low water table in summer, is situated in the upper part of the diagram while the *equisetetosum palustris* (clusters 7–11) is found considerably lower. The subassociation *typicum* (cluster 6) takes an intermediate position. The *Nasturtio-Alopecuretum* (cluster 14) and the *Triglochino-Agrostietum* (clusters 18–22) from sites with a very moist top soil throughout the year, are presented in the lower half of *fig. 5*. The same applies for the brackish communities. While the *Ononido-Caricetum distantis* (cluster 26) and the *Juncetum maritimae* (clusters 27–28) occur in the upper half, the *Agostio-Trifolietum fragiferi* (clusters 23–25) is represented lower down.

The two types of the D.C. of *Festuca arundinacea-[Lolio-Potentillion]* also show this configuration, the drier *Lolium perenne* type (cluster 12) above the wetter *Alopecurus geniculatus* type (cluster 13). The *Triglochino-Agrostietum* subassociation *inops* (cluster 18), having a dry topsoil in summer, is positioned above the two other subassociations. The community of *Scirpus maritimus* and *Alopecurus geniculatus* (cluster 15), a community of low lying parts in pastures inundated for most of the year, is located too high in the diagram.

APPENDIX

Species with presence restricted to class I, with the cluster numbers: Achillea millefolium 2 and 6; Achillea ptarmica 2, 7, 9, 6, 3, 1; Agrostis canina 18; Alisma lanceolatum 7, 9, 6, 3; Alisma plantago-aquatica 9, 6, 15; Allium vineale 2, 12; Alopecurus aequalis 9; Anthoxanthum odoratum 7, 11, 9, 20, 19; Apium graveolens 25; Apium nodiflorum 7, 9; Artemisia maritima 26; Atriplex patula 26; Bidens cernua 19; Bidens frondosa 6; Bidens tripartita 2, 4, 6, 3, 20, 19; Brachythecium velutinum 1; Bryum species 6; Calamagrostis epigejos 23, 24; Capsella bursa-pastoris 6; Carduus crispus

12, 17, 25; Carex acuta 7, 9, 6, 14; Carex arenaria 23, 21; Carex curta 18; Carex ovalis 9; Carex riparia 19; Carex trinervis 26; Centaurea debeauxii ssp. thuillieri 20; Ceratodon purpureus 25; Chamomilla recutita 4; Cicuta virosa 10; Cirsium palustre 23, 26, 28, 19; Cirsium vulgare 12, 25; Convolvulus arvensis 2, 9; Coronopus squamatus 3; Crepis capillaris 4; Dactylis glomerata 12; Danthonia decumbens 16, 18, 23; Deschampsia caespitosa 2, 7, 6; Eleocharis acicularis 4; Epilobium hirsutum 9, 6; Equisetum variegatum 18; Eriophorum angustifolium 7; Eupatorium cannabinum 12; Euphorbia esula 2, 6, 1; Eurhynchium praelongum 19; Filaginella uliginosa 18; Filipendula ulmaria 18,20; Galium aparine 12; Galium mollugo 2; Galium uliginosum 24; Geranium dissectum 9; Herniaria glabra 3; Hippophae rhamnoides 25; Hordeum secalinum 12, 15; Hypochoeris radicata 21; Juncus alpinus 27, 21; Juncus conglomeratus 20; Juncus filiformis 18; Lemna minor 14; Limonium vulgare 23; Linum catharticum 23, 25, 24; Linum usitatissimum 16; Lotus uliginosus 11, 10, 9, 23, 28; Lysimachia vulgaris 9, 6, 1; Lythrum salicaria 2, 7, 11, 9, 4, 6, 18; Matricaria maritima 2, 6, 5, 3; Medicago lupulina 3, 26; Menyanthes trifoliata 23; Myosoton aquaticum 2, 9; Nardus stricta 18; Ophioglossum vulgatum 18, 26, 21, 20; Parapholis strigosa 23, 25, 24; Poa palustris 9; Polygonum mite 10, 9, 6; Polygonum persicaria 11, 13, 18; Potentilla supina 7; Puccinellia distans 16, 12, 17, 15; Radiola linoides 21; Ranunculus circinatus 7, 11, 3; Ranunculus ficaria 2; Rhinanthus angustifolius 5, 21; Rhytidiadelphus squarrosus 18, 25, 21, 19; Rhynchostegiella curviseta 25, 27; Rorippa islandica 2, 7, 17, 9, 6, 3, 14; Rumex x abortivus 6; Rumex acetosa 11, 13, 20; Rumex hydrolapathum 19; Sagina nodosa 26, 24; Salix cinerea 12; Salix triandra 7; Schoenus nigricans 23, 25, 27, 21, 28; Scirpus lacustris ssp. glaucus x triqueter 13; Scirpus setaceus 24; Senecio vulgaris 2; Spergularia marina 16, 14, 23, 21; Spergularia media 12, 17; Symphytum officinale 2, 7, 6, 20, 28; Tanacetum vulgare 3, 1; Thalictrum flavum 2, 7; Trifolium arvense 25, 28; Trifolium dubium 23; Typha latifolia 19; Veronica beccabunga 11, 9, 6; Vicia sativa ssp. nigra 6, 12, 23; Vicia sativa ssp. sativa 12.

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LOLIO-POTENTILLION COMMUNITIES IN IRELAND

K. V. SÝKORA

Botanisch Laboratorium, Afdeling Geobotanie, Toernooiveld, 6525 ED Nijmegen

Very splendid is the bounty of the cattle pond
the Iris is gold because of it.

unknown Irish author, 9th–10th century

SUMMARY

The results of a study of Irish *Lolio-Potentillion* communities are presented in this paper. The syntaxonomical and synecological position of the following communities are described:

1. Basal community of *Agrostis stolonifera-[Lolio-Potentillion anserinae]*
   a) *Lolium perenne-Juncus inflexus* type
   b) *Juncus articulatus-Galium palustre* type
2. *Nasturtio-Alopecuretum geniculati*
   a) *stellarietosum alsinis* subass.nov.
   b) *ranunculetosum scelerati* subass.nov.
3. *Triglochino-Agrostietum stoloniferae*
   a) subassociation *ranunculetosum repentis*
   b) subassociation *juncetosum gerardii*
   c) subassociation *inops*
4. *Agrostio-Trifolietum fragiferi*
   a) subassociation *inops*
   b) subassociation *festucetosum rubrae*

The relations of the communities to the two main environmental factors determining the internal differentiation within the *Lolio-Potentillion* are discussed on the basis of ordination diagrams.

1. INTRODUCTION

This paper is the third in a series presenting the syntaxonomy and synecology of the *Lolio-Potentillion* Tüxen 1947 in a part of Western Europe (SÝKORA 1980, 1982). It reports the results of a study of Irish *Lolio-Potentillion* communities. the field work was carried out in July 1979, mainly along the Irish coast. The locations of the visited sites are indicated in *fig. 1.*

For floristic and ecological reasons this alliance has been separated from the Agropyro-Rumicion Nordhagen 1940 em. Tüxen 1950 (SÝKORA, 1980). The *Lolio-Potentillion* is characterized by the character-species *Agrostis stolonifera, Rumex crispus, Alopecurus geniculatus* and the constant companion *Poa trivialis.* Apart from these the character-species of the *Plantaginetea* Tüxen & Preising 1950, *Potentilla anserina, Plantago major, Lolium perenne* and *Poa annua* are present with often high presence degrees in most or in some of its communities.

Almost all species occurring in this alliance are reptant hemicryptophytes

Fig. 1. Map of Ireland on which the sampling localities are indicated by a square.

and rhizome-geophytes, frequenting soils with a rather high to high phosphorus and nitrogen status (KRUYNE et al. 1967, ELLENBERG 1978), and are tolerant of winter and spring inundation. The *Lolio-Potentillion* is restricted to pastures. For a detailed description of its synecology and syntaxonomy I refer to SÝKORA 1982.

The occurrence of the *Lolio-Potentillion* in Ireland is less extensive than in The Netherlands. This is due to the undulating landscape which is easily

Table 1: Synoptic table of the *Lolio-Potentillion* communities studied in Ireland. In the first column of every cluster the presence class is given. (+ = present only in one relevé; 1 = 1–20%, II = 21–40%; III = 41–60%; IV = 61–80%; V = 81–100%).
In the second column the characteristic coverage is given according to the Braun-Blanquet scale as refined by Barkman et al. (1964).
Communities: cluster 1: Basal community of *Agrostis stolonifera-[Lolio-Potentillion anserinae] Juncus inflexus-Rumex obtusifolius* type.
cluster 2: *Nasturtio-Alopecuretum geniculati stellarietosum alsinis* subass. nov.
cluster 3: Basal community of *Agrostis stolonifera-[Lolio-Potentillion anserinae], Juncus effusus-Holcus lanatus* type.
cluster 4: *Triglochino-Agrostietum* subass. *ranunculetosum repentis*.
cluster 5: idem, subass. *inops*
cluster 6: idem, subass. *juncetosum gerardii*
cluster 7: *Agrostio-Trifolietum fragiferi* subass. *inops*
cluster 8: idem, subass. *festucetosum rubrae*

Species indicated with an asterisk occur twice in the table.

cluster number	1		2		3		4		5		6		7		8	
number of relevés	27		15		22		20		7		9		18		6	
Plantaginetea + Lolio-Plantaginetum																
Potentilla anserina	IV	2m	I	1	III	1	IV	2m	III	1	V	2a	V	3	V	2b
Plantago major	III	1	I	+	+	+	III	+			II	+	IV	1	+	+
* Lolium perenne	IV	1	I	+	I	1	I	+			II	+	+	+		
Poa annua	II	1			II	1	+	1	+	+						
Polygonum aviculare	I	+			I	+										
Lolio-Potentillion character-species and constant companion																
Agrostis stolonifera	V	3	V	2b	V	3	V	2b	V	3	V	3	V	2b	V	2a
Rumex crispus	V	1	IV	1	III	+	IV	+	V	+	IV	+	III	+		
Alopecurus geniculatus	V	2a	V	2b	V	2a	V	2a	V	2m	II	2m	+	+		
c.c. Poa trivialis	V	2b	V	2a	V	2a	V	2a	II	1						
Basal community of Agrostis stolonifera-[Lolio-Potentillion], Lolium perenne-Juncus inflexus type																
* Lolium perenne	IV	1	I	+	I	1	I	+			II	+	+	+		
Juncus inflexus	III	2a	I	2m	I	2b	I	1								
* Elymus repens	III	1	+	+	+	2m					+	1	I	2m		
Nasturtio-Alopecuretum geniculati																
Apium nodiflorum	I	+	V	2m	+	+	III	2m	III	+	III	+				
Nasturtium microphyllum	I	1	IV	1	+	2a	II	+								
Epilobium parviflorum			II	+	I	+	III	+								
Glyceria declinata	+	+	I	1			II	1								
Ranunculus sceleratus			I	+							+	+				
Veronica catenata			+	+												
Constant companion Ranunculo- + Nasturtio-Alopecuretum, differential species Triglochino-Agrostietum ranunculetosum																
Ranunculus repens	V	2b	V	2a	V	2b	V	2b	III	+	II	1				
Triglochino-Agrostietum stoloniferae																
Juncus articulatus	II	+	I	1	III	+	V	1	V	1	III	1	II	1		
Galium palustre	II	+	II	+	IV	+	II	1	IV	1	III	+				
Myosotis laxa ssp. caespitosa	I	1	II	+	I	+	II	+	III	2m						
Ranunculus flammula	+	+	+	+	II	+	III	1	V	1	III	1	I	+		
Carex nigra					I	1	III	1	III	2m	III	2b	+	1		
Hydrocotyle vulgaris					+	+	I	1	III	1	V	2m	I	2m		
Triglochin palustris					+	+	IV	1			III	1	I	1		
Further differentiation																
Holcus lanatus	III	1	III	+	V	1	III	+								
Senecio aquaticus	I	+	II	+	II	1	IV	1	II	+	+	+				
* Myosotis scorpioides			+	+			III	+								
Glyceria fluitans	I	1	III	2m	III	1	III	2m	V	1						
Oenanthe lachenalii	+	+									IV	+	I	+		
Eleocharis uniglumis			+	+	+	1	I	1	+	2a	IV	2m				
Carex otrubae	I	1	I	+	I	+	+	1			III	+	I	+	+	+
Samolus valerandi							I	+			III	1				
Juncus maritimus											II	2a				
Agrostio-Trifolietum fragiferi character- and differential species																
Juncus gerardi							+	2m			IV	1	V	2b	IV	2m
Glaux maritima											II	1	V	1	V	1
Trifolium fragiferum											II	2b	I	1	V	2b

cluster number	1	2	3	4	5	6	7	8
Triglochin maritima						+ +	I +	+ +
Carex distans						+ +	II 2m	V 1
Agrostio-Trifolietum fragiferi festucetosum rubrae + Ononido-Caricetum distantis								
Lotus corniculatus						II +	II 1	V 1
Plantago maritima							II 2m	IV +
Festuca rubra				+ +		+ 2a	I 1	V 2b
Plantago coronopus							III 1	I +
Ranunculo-Alopecuretum geniculati								
* Elymus repens	III 1	+ +	+ 2m			+ 1	I 2m	
* Myosotis scorpioides		+ +		III +				
Carex hirta	II 1		I 1	I 1	+ +	+ 1		
Potentilla reptans	+ +	+ +		+ +		+ +		
Polygonum amphibium	I 1		I 1	+ +				
Equisetum palustre		+ 1	+ +	I +				
Alopecurus pratensis	+ +		+ 2b					
Phalaris arundinacea	I +							
Taraxacum officinale group	I +							
Companion species								
Trifolium repens	IV 2m	III 1	IV 1	V 2m	III +	III 1	II 1	V 2a
Juncus bufonius	II 1	I 1	II 1	IV 1	III 1		II 1	
Juncus effusus	III +	I 1	V 2a	II 1	V 2a	+ +		
Iris pseudacorus	II 2m	II +	II 1	+ +	+ +	+ +		
Eleocharis palustris	I 1	I 1	+ 1	II 1	III 1		I 1	
Leontodon autumnalis	I +		+ +	II 1		IV 1	IV 2m	III +
Calliergonella cuspidata	I 1	+ +	I 1	III 2a	+ +	II +	+ 2b	
Bellis perennis	+ +	+ +	I +	I 1		II 1	I +	
Cardamine pratensis	I 1		I +	I 1	II +	II +		
Cynosurus cristatus	I +	+ +	I 1	II +				
Sagina procumbens	+ +		I +	II 1	+ +	II 1		
Rumex obtusifolius	III 1	II +	+ +	+ +				
Stellaria alsine	I +	III +	II +	II +				
Mentha aquatica		II +	I +	III +		II +		
Cerastium fontanum	I +	+ +	II +	II +				
Cirsium arvense	II +	I +	+ +				+ +	
Carex ovalis	+ 1		I +	+ +	II 1			
Equisetum fluviatile		I +	II 1	I 1				
Ranunculus acris	I +		II +			+ +		
Lythrum salicaria			+ +	+ +		II +	I +	
Leontodon taraxacoides						III 1	II 1	
Juncus acutiflorus			I +		II 1			
Caltha palustris			+ +	II +				
Veronica beccabunga		II +		II +				

Also with presence class I or +: Anagallis tenella (cl. nr. 6), Angelica sylvestris (3, 2), Anthoxanthum odoratum (3), Armeria maritima (7), Aster tripolium (7), Atriplex hastata (7), Brachythecium rutabulum (1, 4), Bromus hordaceus ssp. hordaceus (1), Bryum sp. (1, 7, 6, 4) Calystegia sepium (3), Campylium polygamum (5), Cardamine flexuosa (1, 2), Carex arenaria (1, 7, 6), Carex disticha (1), Carex flacca (4), Cerastium glomeratum (2), Cirsium palustre (1, 3, 2, 4), Cochlearia officinalis (7), Convolvulus arvensis (3), Dactylis glomerata (3), Dactylorhiza incarnata (6), Drepanocladus aduncus (7, 6, 5, 2, 4), Epilobium hirsutum (3), Epilobium obscurum (1, 3), Festuca arundinacea (7, 6, 4, 8), Festuca pratensis (1, 2), Filipendula ulmaria (1, 3, 2, 4), Geranium dissectum (1), Glyceria maxima (1), Glyceria plicata (4), Hypericum tetrapterum (4), Lotus uliginosus (1, 3, 7, 6, 5, 2), Matricaria perforata (1), Matricaria maritima (7), Mentha arvensis (1, 2), Odontites verna ssp. serotina (3), Oenanthe crocata (3), Dactylorhiza maculata (3), Phleum pratense (1, 2), Phragmites australis (3, 2), Plantago lanceolata (1, 4), Poa pratensis (7, 6), Polygonum hydropiper (1, 3, 2, 4), Potentilla palustris (5), Prunella vulgaris (1, 3, 4), Pulicaria dysenterica (3), Rhynchostegiella curviseta (7, 6), Rumex acetosa (3), Rumex conglomeratus (1, 3), Salix repens (7), Scirpus lacustris ssp. lacustris (5), Scirpus maritimus (1, 6, 2), Senecio erucifolius (1), Spergularia marina (7), Stachys palustris (1), Stellaria graminea (1, 3), Stellaria media (1, 2), Symphytum officinale (3), Trifolium dubium (1, 3), Trifolium pratense (1, 3), Urtica dioica (1, 3, 2), Veronica scutellata (5, 4), Veronica anagallis-aquatica (2).

drained naturally or artificially, the absence of long rivers with wide river forelands, the steepness of its coasts and the low nutrient status of a part of Ireland, which is covered by peat bogs (About 15% of the total surface) and moorland (PRAEGER 1934, WEBB 1952, WHITTOW 1974).

2. METHODS

Hundred and twenty four relevés (*table 1*) were made on the basis of the principles of the French-Swiss school of phytosociology (WESTHOFF & VAN DER MAAREL 1973). Sample plot size, site selection and habitat description are conform SÝKORA 1982. The raw table was structured by means of the Tabord program (VAN DER MAAREL et al. 1978, VAN DER MAAREL 1979). The similarity ratio (WISHART 1969) was used to measure similarities between relevés and clusters. In the definite table the threshold value was 0.40 and the fusion level 0.77. One relevé was relocated by hand from cluster 2 tot cluster 1, one from cluster 1 to 2 and another from the rest-group to cluster 6. In this paper only the synoptic table is presented.

Both the relevés and the cluster centroids were used in a principal components analysis according to the Ordina program (ROSKAM 1971). Plant nomenclature follows the Flora Europaea (TUTIN et al. 1964–1980) for phanerogams and LANDWEHR (1966) for bryophytes.

3. STATUS OF THE ALLIANCE IN RELATION TO THE CONTINENT

The *Ranunculo-Alopecuretum geniculati* Tüxen 1937 has not been observed in Ireland during the present study. As can be seen in *table 1* the character-species *Potentilla reptans, Carex hirta, Rorippa sylvestris* and *Mentha pulegium* and the differential species *Phalaris arundinacea, Polygonum amphibium, Taraxacum officinale* (group), *Elymus repens, Lysimachia nummularia, Myosotis scorpioides, Rorippa amphibia, Alopecurus pratensis, Equisetum palustre, Glechoma hederacea* and *Glyceria maxima,* are either absent or present with a low presence degree. *Juncus compressus* and *Inula britannica* are absent from Ireland and *Mentha pulegium* is very rare (WEBB 1967). Because of the special topographic conditions in Ireland and the absence of wide rive forelands, the *Ranunculo-Alopecuretum,* being restricted to sites with a highly dynamic water table, with inundation water that can be several meters deep and a water table that in summer drops sufficiently deep to allow desiccation of the top soil, is very rare or possibly even absent. Besides desiccation is less frequent by the constancy of atmospheric moist the even distribution of the rainfall throughout the year and from year to year (WEBB 1952). Because of these climatic characteristics the effluence of the rivers is more or less equally distributed over the year. These conditions are unfavourable for the *Ranunculo-Alopecuretum,* especially for the subassociation *rorippetosum sylvestris,* which is confined to sites with a low ground water table during the summer. *Rorippa sylvestris,* a species highly indicative for these circumstances, is rare in Ireland.

4. THE PLANT COMMUNITIES (*table 1*)

4.1. Basal community of *Agrostis stolonifera-[Lolio-Potentillion anserinae], Juncus inflexus-Rumex obtusifolius* type (cluster 1)

Fig. 2. Basal community of Agrostis stolonifera- [Lolio-Potentillion anserinae] occurring on the bank of a brook (grazed patch on the right side of the picture.)

From all the communities described in this paper the basal community of *Agrostis stolonifera-[Lolio-Potentillion anserinae], Juncus inflexus-Rumex obtusifolius* type (cluster 1) has the strongest affinity to the *Ranunculo-Alopecuretum*. It is differentiated from the other Irish communities by *Lolium perenne, Juncus inflexus* and *Elymus repens*. As it clearly belongs to the *Lolio-Potentillion* but cannot be assigned to one of its associations, because character-species and sufficient differential species are lacking, it is here described as a basal community according to the deductive method of KOPECKÝ & HEJNÝ (1974, 1978). Two other types of this basal community have been described for The Netherlands (viz. the *Trifolium fragiferum-Ranunculus sardous* type and the *Scirpus maritimus-Juncus bufonius* type) (SÝKORA, 1982). The *Juncus inflexus-Rumex obtusifolius* type is different from the other types by the presence of *Juncus inflexus, Elymus repens* and *Rumex obtusifolius* with presence class III. It has been found mainly on heavy clay and a few times on sandy clay. The soil was often very hard by desiccation and spots of rust indicating the temporarily waterlogged conditions were clearly visible. The basal community occurred on lower parts of pastures, in drainage furrows, along ditches and brooks with running water and on the bottom of a totally drained lake. Like in The Netherlands the basal community of *Agrostis stolonifera* was found on severely poached sites. The clay soils in Ireland are often partly waterlogged, even when on a fairly steep slope, resulting in encroachment by rushes (WEBB,

Fig. 3. The Triglochino-Agrostietum stoloniferae ranunculetosum repentis along a rivulet. As banks are absent, water continually seeping sideways is keeping the soil moist throughout the year. Iris encoachment is a common feature in Irish pastures.

1952, O'SULLIVAN 1968). *Juncus inflexus,* as a calcicole species, is indicating the alkalinity of the soil.

Elymus repens, being a differential species of the *Ranunculo-Alopecuretum geniculati rorippetosum sylvestris,* is indicative of a low water table and a dry top soil during the summer season. *Rumex obtusifolius,* a character-species of the *Artemisietea vulgaris* Lohm., Prsg. & Tüxen 1950, has its highest presence on alkaline (pH water > 7.00), nutrient rich soils, with a high nitrogen and phosphorus status (p-citric acid > 80) (CAVERS & HARPER 1964, KRUYNE et al. 1967, WESTHOFF & DEN HELD 1969, OBERDORFER 1970). I do not agree with the statement of HÜLBUSCH (1969) that *Rumex obtusifolius* has to be considered a character-species of the *Lolio-Potentillion* (called *Agropyro-Rumicion* by him). The distinction of the association *Poo triviali-Rumicetum obtusifolii* Hül-

Fig. 4. The Agrostio-Trifolietum fragiferi subassociation inops as found on the shore of a salt lake. It is extensively grazed by sheep.

busch 1969 is insufficiently founded. For the synecology of the *Juncus effusus-Holcus lanatus* type (cluster 3) differentiated by *Juncus effusus* (presence class V) and *Holcus lanatus* (presence class V) see section 4.4.

4.2. *Nasturtio-Alopecuretum geniculati* Sýkora 1982.
Subassociation nov. *ranunculetosum scelerati* and subassociation nov. *stellarietosum alsinis* (cluster 2).

Within the *Lolio-Potentillion* the *Nasturtio-Alopecuretum* is the association with some floristic relation to the swamp alliance *Glycerio-Sparganion,* mainly consisting of helophytes (OBERDORFER 1977). In the Netherlands where the association has been described (SÝKORA 1982), it is characterized by the character-species of the order and alliance as well as by a number of differential species. In Ireland the association presents itself in a somewhat impoverished form. Because of the presence of *Nasturtium microphyllum,* character-species of the *Nasturtietum officinalis* Seib. 1962, cluster 2 should be assigned however, to the *Nasturtio-Alopecuretum.*

It appears moreover, that the Irish form of the association contains *Apium nodiflorum* as a second differential species (presence class V) against the other Irish communities. *Apium nodiflorum,* likewise a swamp helophyte, is a character-species of the *Helosciadetum nodiflori* Br.Bl. 1931. *Apium nodiflorum,* being rather rare in The Netherlands (ARNOLDS et al. 1975, VAN DER MAAREL 1971), is frequent in Ireland. As a species with mainly a mediterranean-subatlantic

distribution it reaches its northern limit in The Netherlands (TUTIN et al. 1968). This may be responsible for its absence in the Dutch relevés.

From the continental form of the *Nasturtio-Alopecuretum* the Irish community is differentiated not only by the constant presence of *Apium nodiflorum* but furthermore by the presence of *Holcus lanatus* (presence class III) and *Stellaria alsine* (presence class III) and the absence or lower presence of *Potentilla anserina, Plantago major, Eleocharis uniglumis, Ranunculus sceleratus, Veronica catenata* and *Ranunculus sardous*. In the previous publication (SÝKORA 1982) the Dutch form of the *Nasturtio-Alopecuretum* has not been subdivided. For the difference mentioned above, it is now possible to distinguish two subassociations. The Dutch material is described here as the subassociation *ranunculetosum scelerati* subass.nov., the Irish community as the subassociation *stellarietosum alsinis* subass.nov.

The subassociation *ranunculetosum* occurs on nutrient-rich, basic soils. *Ranunculus sceleratus* is a character-species of the *Ranunculo-Rumicetum maritimi* Siss. (1946) 1966, a community of very nutrient-rich soils (WESTHOF & DEN HELD 1969, VAN DER TOORN 1980). *Ranunculus sardous* has its highest relative average frequency in pastures on alkaline (pH water > 7) soils (KRUYNE et al. 1967). It is absent on strongly acid and moderately acid soils and very infrequent on weakly acid soils (pH water respectively < 5.05, 5.05–5.50 and 5.55–6.00).

The subassociation *stellarietosum alsinis* is restricted to less nutrient-rich, moderately acid soils. It has some affinity to the *Montio-Apietum nodiflori* (MAAS 1959) SEGAL & WESTHOFF 1969, which occurs along clear, nutrient- and calcium-poor rivulets. According to ELLENBERG (1978) *Stellaria alsine* is indicative for sites where the soil is between acid and moderately acid and between nitrogen-poor and moderately nitrogen-poor. The *Nasturtio-Alopecuretum stellarietosum alsinis* has been found on very soft, reduced clay along ditches, pools and in drainage furrows.

4.3. *Triglochino-Agrostietum stoloniferae* Konczak 1968 (cluster 4–6) and basal community of *Agrostis stolonifera-[Lolio-Potentillion anserinae], Juncus effusus-Holcus lanatus* type (cluster 3).

The *Triglochino-Agrostietum* is restricted to pastures occurring on moderately acid soils with a low nutrient status. Consequently it is highly susceptible to fertilization. It is characterized by *Triglochin palustris* (character-species) and *Juncus articulatus, Galium palustre, Ranunculus flammula, Hydrocotyle vulgaris, Carex nigra, Myosotis laxa* ssp. *caespitosa* (differential species against the other Irish associations).

The subassociation *ranunculetosum repentis* (*table 1*, cluster 4), characterized by the presence of *Ranunculus repens* and (in the Dutch relevés) also by *Lolium perenne*, is confined to marshy soils uninfluenced by salt. In Ireland it has been found on soft, moist clay mixed with organic material, in depressions in pastures, along rivers and rivulets, on a lake shore and in a ditch without standing water.

The high presence degree of *Senecio aquaticus, Holcus lanatus* and *Myosotis scorpioides* indicates that this community is grazed extensively only. While *Senecio aquaticus* has its highest relative average frequency on pure hayfields, *Holcus lanatus* and *Myosotis scorpioides* are found most frequently on hay pastures (KRUYNE et al. 1967). On the continent *Senecio aquaticus* is a character-species of the *Senecioni-Brometum racemosi* R.Tx. & Preising 1951, a community from moist, sometimes also slightly grazed hayfields on calcium-poor soils (WESTHOFF & DEN HELD 1969). In Ireland it is a character-species of the *Senecioni-Juncetum acutiflori* Braun-Blaquet & Tüxen 1952, a community occurring on soils with a high water retention capacity and a low to moderate base status.

On pastures with slightly brackish soils the subassociation *juncetosum gerardii* (cluster 6) has been recorded. Differential species of this subassociation are *Juncus gerardi* and *Glaux maritima* (see SÝKORA 1982). It is differentiated against the other *Lolio-Potentillion* communities found in Ireland by *Eleocharis uniglumis, Oenanthe lachenalii, Carex otrubae, Samolus valerandi* and, with presence class II, *Juncus maritimus. Oenanthe lachenalii* and *Juncus maritimus* are character-species of the *Juncetum maritimi* Bilik 1956, a community found on brackish, extensively grazed higher salt marshes. The subassociation *juncetosum gerardii* was recorded in Ireland on sandy soils mostly covered with a 3 to 10 cm top soil very rich in organic material. It occurs on the shore of salt lakes connected to the sea by a narrow inlet and on the banks of a river and a brook near the sea coast.

Both the *Triglochino-Agrostietum* subassociation *inops* (cluster 5) and the basal community of *Agrostis stolonifera-[Lolio-Potentillion], Juncus effusus-Holcus lanatus* type (cluster 3) have been found on small, grazed, open patches in pastures dominated by *Juncus effusus*. While in the subassociation *inops* all differential species of the *Triglochino-Agrostietum* are present with a high presence class, these species are restricted to *Juncus articulatus* and *Galium palustre* in the basal community. The ground between the ungrazed and untrampled rush clumps is subject to heavy grazing and trampling resulting in openings in the field-layer. As *Juncus effusus* seedlings are extremely susceptible to competition from other plants, establishment of the species depends on these patches of bare soil (AGNEW 1961). Poaching has its most severe effects under winter grazing conditions. While in the subassociation *inops* trampling intensity is still sufficiently low to permit the presence of the differential species, they are excluded from the basal community by the severe poaching. Both communities have been found on clay, the basal community under drier conditions. Under still drier conditions the *Centaureo-Cynosuretum* Braun-Blanquet & Tüxen 1952 subassociation of *Juncus effusus* (O'SULLIVAN 1968) will develop.

4.4. *Agrostio-Trifolietum fragiferi* Sýkora 1982 (cluster 7 and 8)

The *Agrostio-Trifolietum fragiferi* subassociation *inops* (SÝKORA 1982) as found in Ireland (cluster 7) is differing from the Dutch subassociation *inops* by the absence of *Eleocharis uniglumis* (presence class IV in the Dutch table) and the higher presence of *Plantago major, Rumex crispus, Plantago coronopus* and

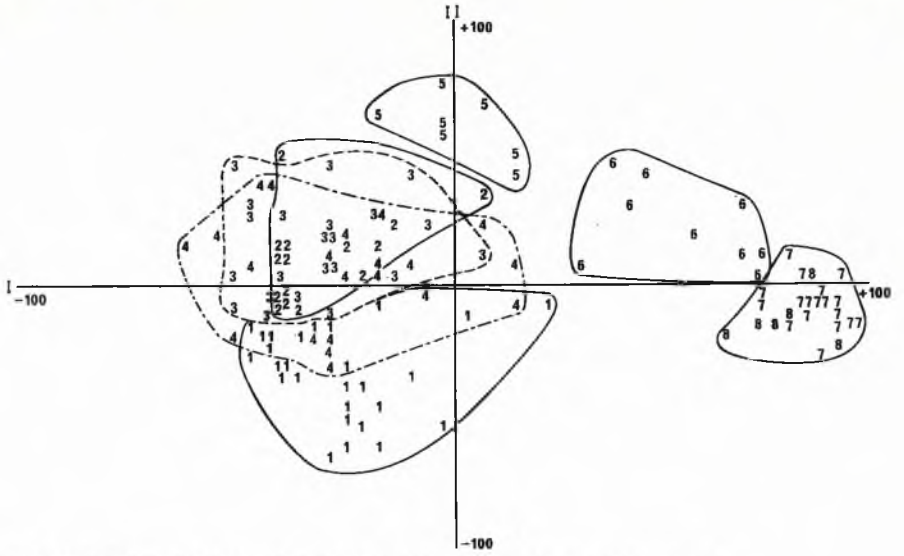

Fig. 5a. P.C.A. ordination of all relevés along the first and second dimension.

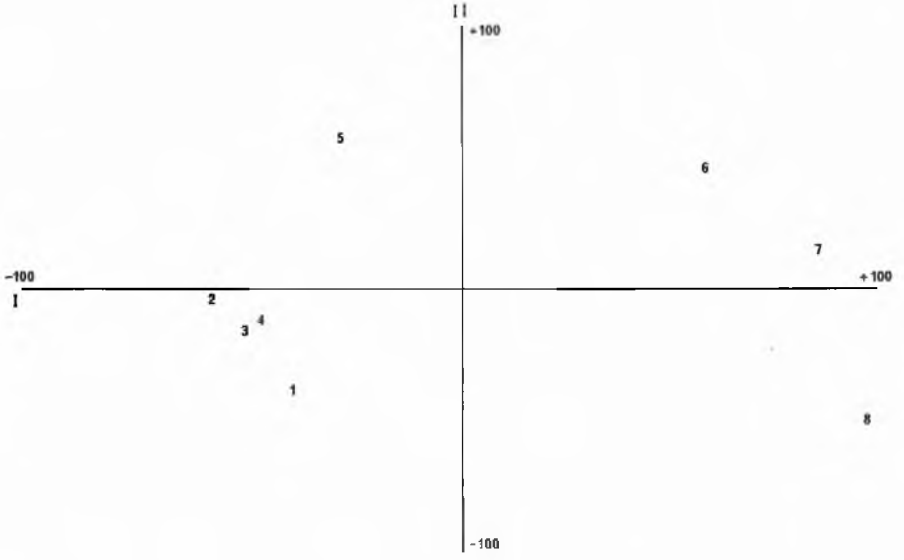

Fig. 5b. Ordination of the centroids of the clusters presented in *table 1*.

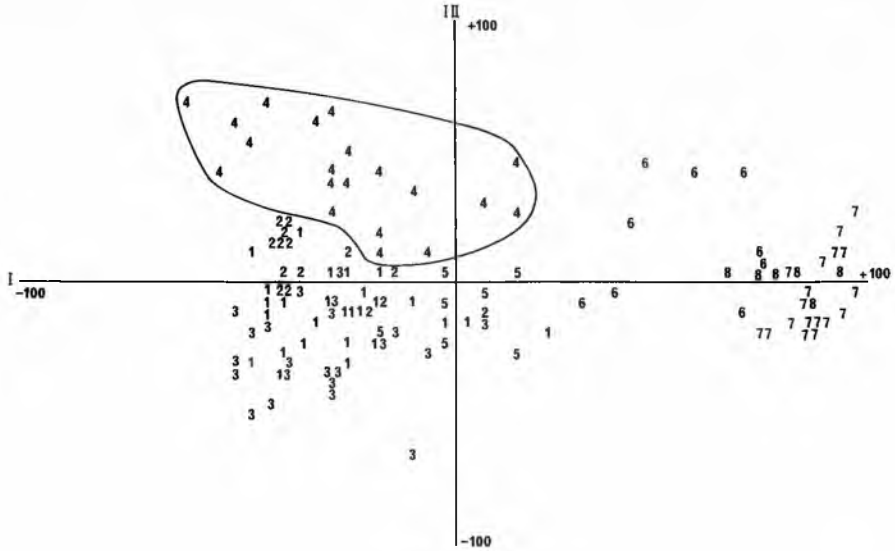

Fig. 5c. Ordination of the relevés composing the clusters in *table 1* along the first and third dimension. The numbers correspond to the cluster numbers used in *table 1*.

Leontodon autumnalis. Like in The Netherlands this community is characterized by the very low grazing pressure. It is found under drier conditions than the Dutch community. It occurs on the shores of salt lakes in connection with the sea by a narrow inlet. The vegetation is considerably influenced by salt spray and often, during periods with sufficient wind velocity, foam of the sea is blown into the vegetation. Inundation with sea water occurs during extreme high tide. The subassociation *inops* has been found on gravelly sand and on pure sand, in a few cases covered by a layer of silt.

Cluster 8 can be assigned to the *Agrostio-Trifolietum fragiferi festucetosum rubrae*, characterized by *Trifolium fragiferum* (character-species) and *Juncus gerardi, Glaux maritima, Plantago maritima, Festuca rubra* and *Carex distans* (differential species). Unlike the Dutch material *Centaurium pulchellum, Holcus lanatus, Poa pratensis, Cerastium fontanum* and *Odontites verna* ssp. *serotina* are absent. *Lotus corniculatus* however has a higher presence class in Ireland (V) than in The Netherlands (presence class I) where it is a differential species for the *Ononido-Caricetum distantis* Runge 1966. The latter community has only been recorded from the Wadden islands and along the coast of the Baltic sea. It forms a zone above the *Agrostio-Trifolietum fragiferi festucetosum rubrae*, on small dunes occurring in extensively grazed upper salt marshes on the Wadden islands and along the coasts of the Baltic sea. This might be an indication that the *festucetosum rubrae* from *table 1* is confined to drier soils when compared to the *festucetosum rubrae* of the Dutch material. The data from KRUYNE et al. (1967) showing that *Lotus corniculatus* has by far the highest relative average frequency on dry soils are in accordance with this suggestion.

The Irish variant, to be named variant with *Lotus corniculatus*, was found on small dunes on an old race course now turned into a salt marsh by a dike burst. The soil consisted of sand with a top soil of about 10 cm silt mixed with some organic material.

5. Principal Components Analysis

Figures 5a and *c* are the result of the ordination of the separate relevés. In *fig. 5b* an ordination of the cluster centroids is represented. The percentage extracted variance values of the first two axes are respectively 24 and 8 for *fig. 5a* and 51 and 15 for *fig. 5b*. The percentage extracted variance for the third axis (*fig. 5c*) is 7. The *figures 5a* and *b* show a similar arrangement of the clusters. Dimension I corresponds with a gradient in salt influence, the *Triglochino-Agrostietum juncetosum gerardii* (cluster 6) being intermediate between the *Agrostio-Trifolietum fragiferi inops* and *festucetosum rubrae* (cluster 7 and 8) from brackish soils and the *festucetosum rubrae* (cluster 7 and 8) from brackish soils and the *Triglochino-Agrostietum inops* and *ranunculetosum repentis* (cluster 5 and 4), the basal community of *Agrostis stolonifera-[Lolio-Potentillion], Juncus effusus-Holcus lanatus* type (cluster 3) the *Nasturtio-Alopecuretum* (cluster 2) and the basal community of *Agrostis stolonifera-[Lolio-Potentillion], Juncus inflexus-Rumex obtusifolius* type (cluster 1), all from fresh soils.

Dimension II arranges the communities according to the moisture content of the soil during the summer season. On fresh soils the *Nasturtio-Alopecuretum geniculati* (cluster 2), the basal community of *Agrostis stolonifera-[Lolio-Potentillion], Juncus effusus-Holcus lanatus* type (cluster 3) and the *Triglochino-Agrostietum ranunculetosum repentis* (cluster 4) are placed intermediate between the relatively dry basal community of *Agrostis stolonifera-[Lolio-Potentillion], Juncus inflexus-Rumex obtusifolius* type (cluster 1) and the wet *Triglochino-Agrostietum* subassociation *inops* (cluster 5). In a brackish environment the sequence from relatively dry to wet is represented by *Agrostio-Trifolietum fragiferi festucetosum rubrae* (cluster 8), followed by the subassociation *inops* (cluster 7) and ended by the *Triglochino-Agrostietum juncetosum gerardii* (cluster 6). The two subassociations of the *Agrostio-Trifolietum* (clusters 7 and 8) have only been separated clearly in *fig. 5b*, the ordination diagram of the cluster centroids. In *fig. 5a* the two overlapping clusters 3 and 2 are clearly separated from clusters 1 and 5. Cluster 4 having a broad overlap with clusters 1, 2 and 3 along the second dimension, is clearly separated from these communities along the third dimension. Although the second dimension can be interpreted ecologically without difficulty, interpretation of the third dimension (*fig. 5c*) is less easy. Possibly the separation of cluster 4 from the clusters 1, 2 and 3 reflects its lower nutrient status. It is certainly less disturbed by poaching and grazing pressure is lower in comparison to these communities. From the ordination diagrams can be concluded that the main factors for the internal differentiation of the Irish *Lolio-Potentillion* are the water content of the soil during the summer season and the influence of salt. The same conclusion was reached in The Netherlands (Sýkora 1982).

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LOLIO-POTENTILLION COMMUNITIES IN BELGIUM AND NORTH-WESTERN FRANCE

K. V. SÝKORA

Botanisch Laboratorium, Afdeling Geobotanie, Toernooiveld, 6525 ED Nijmegen

SUMMARY

The ecology and the syntaxonomy of the following Belgian and French *Lolio-Potentillion anserinae* communities are described:

1. *Ranunculo-Alopecuretum geniculati*
2. Basal community of *Agrostis stolonifera*-[*Lolio-Potentillion anserinae*]
   a) *Juncus inflexus-Carex otrubae* type
   b) *Eleocharis uniglumis-Carex otrubae* type
   c) *Trifolium fragiferum-Carex hirta* type
3. *Triglochino-Agrostietum stoloniferae ranunculetosum repentis*
4. *Nasturtio-Alopecuretum geniculati ranunculetosum scelerati*
5. *Agrostio-Trifolietum fragiferi*

a) subassociation *typicum*
b) subassociation *inops*

The syntaxonomical position of *Carex otrubae* and *Eleocharis uniglumis* is discussed, leading to the conclusion that both species are character-species of the association group with *Eleocharis uniglumis*.

The two main ecological factors are elucidated with the help of a P.C.A. ordination diagram.

1. INTRODUCTION

During June and July 1980 Belgium and North-Western France were visited in order to study the *Lolio-Potentillion anserinae* Tüxen 1947. This alliance has been separated from the *Agropyro-Rumicion cripsi* Nordhagen 1940 on floristic and ecological criteria (SÝKORA 1980). It occurs in pastures inundated during winter and spring on nutrient-rich to moderately nutrient-poor soils. The main factors responsible for the internal differentiation of the *Lolio-Potentillion* are the hydrological situation in summer, the influence of salt and the nutrient status of the soil. Communities belonging to the *Lolio-Potentillion* in The Netherlands and in Ireland have been described earlier (SÝKORA 1982a, b). For a detailed description of the synecology of this alliance I refer to these papers.

In Belgium most relevés were made along former creeks now surrounded by reclamations in the Flemish polder area. The French relevés were made on the banks of the rivers Liane, Canche, Authie and Somme, and in the Marais de Balançon and the Marais de Favières.

Eighty five percent of the Flemish polders is old or medium aged. The draining following the reclamation (7th, 8th, 11th and 12th century) caused compaction of the peat and as a consequence the soil level was lowered considerably. This worsened the drainage situation, so that the polders can be utilized as pastures only. After the reclamation the existing creeks and their branches were

used as a basis for the drainage system. The resulting sinuous drains are easily obstructed; besides they are shallow, making drainage less efficient (VANHECKE 1977). Fluctuations of the water-level with 50 cm or more, the high nutrient status of the soil and the presence of cattle explain the frequent occurrence of the *Lolio-Potentillion* along the Flemish creeks. The water of these creeks is sometimes brackish due to the presence of late Atlantic and Subboreal saliferous peat layers on a depth of 1–5 m below Ordnance Datum and the seepage of salt-containing ground water. The salt enrichment of the peat was caused by inundation of it with sea water during transgressions of the sea in the early part of the christian era (DE RIDDER 1957, VISSCHER 1975, BIJHOUWER 1977, BRAND 1978, GUERLESQUIN & WATTEZ (1979), ANONYMUS (1979). The moist grasslands along the creeks have a high ornithological significance (BECUWE 1977, HOUWEN 1977, ANONYMUS 1979).

Because of the hilly character of North-Western France the *Lolio-Potentillion* is restricted to the riversides and the marshes near the mouth of the rivers. The rivers in this area are running from south-east to north-west. As a consequence of the relative shortness of these rivers, the small size of the watersheds and the artificially improved discharge, water fluctuations are considerably less pronounced than in the river-bed of, for instance, the Rhine and the Waal.

As an important part of the riversides are either well drained or ungrazed (resulting in extensive reed-swamps used for shooting water-fowl) the *Lolio-Potentillion* is well developed only locally, for instance along ponds resulting from the cutting of peat, along ditches and drainage furrows and in low lying parts of pastures with impeded drainage. The presence of *Lolio-Potentillion* communities in North-Western France has been previously recorded by GÉHU (1961), GÉHU & WATTEZ (1965), FRILEUX & GÉHU (1975), WATTEZ (1967, 1975), FRILEUX (1976) and BOURNERIAS et al. 1976.

The vegetation of humid grasslands inclusive the *Lolio-Potentillion* has been severely degraded by drainage, intensification of agricultural practices e.g., use of herbicides, overfertilization, overstocking with cattle, termination of grazing, the planting of poplars, the canalization of the rivers and industrialization (WATTEZ 1975, FRILEUX & GÉHU 1975, FRILEUX 1976).

2. METHODS

The methods were the same as described in SÝKORA 1982b (this issue, p. 189)

3. STATUS OF THE ALLIANCE IN BELGIUM AND NORTH-WESTERN FRANCE.

In Western Germany and The Netherlands the most characteristic and best developed association of the *Lolio-Potentillion* is the *Ranunculo-Alopecuretum geniculati*. It is the first association which has been described and it can be considered as the 'type-association' of the alliance. However, none of the communities presented in this paper can be assigned to the *Ranunculo-Alopecuretum*. Only *Carex hirta* (character-species for this association), *Equisetum palustre*

Table 1. Synoptic table of the *Lolio-Potentillion* communities studied in Belgium and North-Western France. In the first column of every cluster the presence class is given (+ = present only in one relevé; I = 1–20%; II = 21–40%; III = 41–60%; IV = 61–80%; V = 81–100%).
In the second column the characteristic coverage is given according to the Braun-Blanquet scale as refined by BARKMAN et al. (1964).
Communities: clusters 1, 2 and 4: Basal community of Agrostis stolonifera-[Lolio-Potentillion anserinae], Eleocharis uniglumis-Carex otrubae type (cluster 1); Juncus inflexus-Carex otrubae type (cluster 2); Trifolium fragiferum-Carex hirta type (cluster 4). Triglochino-Agrostietum stoloniferae ranunculetosum repentis (cluster 3).
clusters 5 and 6: Nasturtio-Alopecuretum geniculati ranunculetosum scelerati, variant with Oenanthe fistulosa (cluster 5) and variant with Juncus gerardi (cluster 6).
clusters 7 and 8: Agrostio-Trifolietum fragiferi, subass. typicum (cluster 7) and subass. inops, variant with Poa trivialis (cluster 8).

cluster number	1		2		3		4		5		6		7		8	
number of relevés	6		12		20		52		15		20		7		5	
Plantaginetea + Lolio-Plantaginetum character-species																
Potentilla anserina	+	2m	V	2m	IV	2m	IV	1	II	1	V	1	III	2m	III	1
Plantago major	III	+	II	+	III	+	IV	+	IV	+	IV	1	V	1	IV	1
Lolium perenne			II	+	II	+	III	1	III	1	I	+	III	+	IV	1
Poa annua							I	1								
Polygonum aviculare			I	+			I	+			I	+				
Lolio-Potentillion, character-species + constant companion																
Agrostis stolonifera	V	2b	V	3	V	3	V	3	V	3	V	3	V	3	V	3
c.c. Poa trivialis	V	2b	IV	2a	IV	2a	V	2b	V	2m	II	2m	III	1	V	1
Alopecurus geniculatus	V	2m	III	1	V	2b	V	2a	V	2b	V	2b	IV	1		
Rumex crispus	V	+	III	+	II	+	III	+	II	+	III	+	III	+	+	+
Juncus inflexus			V	2a	IV	1	II	+	II	2m			III	1		
Ranunculo-Alopecuretum, character- and differential species																
Taraxacum officinale group	IV	1	I	+	I	+	I	+					+	+	+	+
Equisetum palustre			III	+	III	1	I	1					+	+		
Carex hirta			I	2m	IV	1	III	1	I	1	I	2m				
Elymus repens	II	1	I	1			I	1			II	1	+	+		
Lysimachia nummularia			II	1	I	+	I	1	+	1	I	+				
Polygonum amphibium			II	1	II	1	I	1								
Potentilla reptans	+	+	I	1			+	+								
Rorippa amphibia							+	+			+	+				
Phalaris arundinacea							I	+								
Myosotis scorpioides							I	1								
Glyceria maxima							I	1								
Association group with Eleocharis uniglumis; character- and differential species.																
Carex otrubae	V	+	V	1	III	+	II	+	III	1	II	+	V	1	+	+
Phragmites australis	III	2m	V	1	I	1	II	1	III	1	II	1	V	2m		
Eleocharis uniglumis	V	2a	II	2a	+	1	I	2m	+	1	II	1	+	1		
Triglochino-Agrostietum, character- and differential species																
Juncus articulatus	III	1	III	+	V	1	III	1	II	1	II	1	V	2m	+	+
Galium palustre	II	+	IV	+	III	+	III	1	+	+	I	+				
Triglochin palustris			+	1	III	1	I	1	II	1	III	2m			III	1
Ranunculus flammula					III	1	I	1								
Carex nigra					II	1	+	2a								
Hydrocotyle vulgaris					+	1	I	1			II	1				
Myosotis laxa ssp. caespitosa	+	+	+	+	+	+	II	1	I	+						
Nasturtio-Alopecuretum																
Ranunculus sceleratus			+	+			II	+	III	+	III	+	+	+	II	1
Nasturtium microphyllum			II	+	I	1	II	+	II	+	IV	1			+	+
Apium nodiflorum			+	+	III	1	II	1	II	1	III	1	II	+	+	+
Veronica catenata					I	1	I	+	+	+	III	+	II	+		
Ranunculus sardous			I	+	I	+	I	+	III	1	+	1				
Glyceria declinata			+	1	II	1	II	1	III	1	I	1				
Epilobium parviflorum			+	+	II	+	II	+			I	+	II	1		
Agrostio-Trifolietum fragiferi																
Trifolium fragiferum	+	2m	I	1	IV	2m	III	1	IV	1	III	1	V	1	V	2m
Juncus gerardi			I	2m	II	1	I	1	I	2m	IV	1	V	2m	IV	2a
Carex distans					II	+							III	2m	IV	1
Lotus tenuis					II	1							IV	+		
Centaurium pulchellum													II	+		

cluster number	1	2	3	4	5	6	7	8
Glaux maritima					I 1	+ 1		III 2m
Festuca rubra		+ 1	I 1					III 2m
Triglochin maritima								+ +
Further differentiation								
Festuca pratensis	V 1	I +	II +	I +	+ +	+ +		
Glyceria fluitans	V 1	II 1	II 1	II 1		I 2m	II +	
Oenanthe fistulosa	V 1	+ 1	II +	II 1	III 1	I +	+ +	
Bromus racemosus	II +							
Cardamine pratensis	IV 1	III +	IV 1	I +				
Carex disticha			II 1					
Bellis perennis			I +	I +	+ +		V 1	
Carex flacca				I 1			IV 1	
Pulicaria dysenterica		II 1	II +	I +			IV +	
Leontodon autumnalis			+ +	I +			III +	
Salix repens							III +	
Festuca arundinacea	+ +	+ +	+ +	+ +				V 2a
Companion species								
Ranunculus repens	V 2a	V 1	V 2a	V 2a	IV 1	III 1	IV 1	+ +
Trifolium repens	IV 2m	III 1	I 1	V 1	II 1	II +	IV 1	IV 2m
Juncus bufonius group	+ 1	+ 1	I 2m	II 1	II 1	II 1	III 1	II 1
Drepanocladus aduncus	III 2a	+ +	III 2a	I +	I +	I 1	V 2m	+ 1
Mentha aquatica		IV 1	III +	III 1	I +	I 2m	V 1	+ +
Rumex conglomeratus	+ +	III +	III +	II +	I 1	I 1		
Scirpus maritimus		I 1	I 2m	I 1	II 1	III 1		IV 1
Cerastium fontanum	+ +		I +	II +	+ +		+ +	
Holcus lanatus	III 1	II +	II +	II 1				+ +
Eleocharis palustris		I 1	III 2m	II 2m		III 2m	I 1	
Atriplex hastata				I 1	I +	III 1		II +
Equisetum arvense		+ +	I +	+ +			II 1	
Phleum pratense	II +		I 1	I +		+ +		
Senecio aquaticus		+ +	II +	I +		+ +		
Odontites verna ssp. serotina		II 1	I +	I 1				
Veronica beccabunga			I 1	II +	+ +			
Brachythecium rutabulum	III 1			I +				
Calliergonella cuspidata			II +	I 1				
Chenopodium rubrum				I +	II +	II 1		

Species with presence class I or +: Alisma plantago-aquatica (cluster number 6), Arrhenatherum elatius (2), Aster tripolium (4, 6, 8), Atriplex patula (4), Berula erecta (2, 4), Bidens cernua (4), Bidens tripartita (6, 4), Carex acutiformis (4), Carex riparia (5, 4), Catabrosa aquatica (4), Cirsium arvense (2, 6, 4, 1), Cynosurus cristatus (4), Epilobium hirsutum (2), Epilobium obscurum (3), Epilobium palustre (2), Equisetum fluviatile (4), Filipendula ulmaria (4, 3), Hippuris vulgaris (4, 6), Hordeum secalinum (5, 6, 4), Iris pseudacorus (2, 4), Juncus acutiflorus (4), Juncus effusus (4), Lychnis flos-cuculi (4), Lycopus europaeus (2, 6, 3), Lythrum salicaria (7, 6), Medicago lupulina (6), Myosoton aquaticum (4), Oenanthe aquatica (5, 7, 6, 4), Poa pratensis (8), Polygonum hydropiper (4), Polygonum mite (2, 6, 4, 3), Prunella vulgaris (4, 3), Puccinellia distans (6, 4), Ranunculus acris (4, 3), Rhynchostegiella curviseta (4), Rumex obtusifolius (4), Rumex palustris (5, 6), Sagina procumbens (4), Samolus valerandi (2, 6, 4, 8), Scirpus lacustris ssp. tabernaemontani (5, 6, 4, 3), Scirpus setaceus (4), Solanum dulcamara (2, 4), Spergularia marina (6), Stellaria alsine (4), Stellaria media (2, 4), Symphytum officinale (6, 4), Trifolium pratense (2, 4), Urtica dioica (2, 4).

and *Taraxacum officinale* group (differential species) are present with presence class III or more. The character-species *Potentilla reptans, Rorippa sylvestris, Juncus compressus, Inula britannica, Mentha pulegium* and the differential species *Phalaris arundinacea, Polygonum amphibium, Elymus repens, Lysimachia nummularia, Myosotis scorpioides, Rorippa amphibia, Alopecurus pratensis, Glechoma hederacea* and *Glyceria maxima* are absent or are present with presence class II or less.

The ecological explanation for this phenomenon can be found in the hydrology of the Flemish creeks and the French riversides. Because of insufficient fluctuation of the water-level, no sites with prolonged inundation followed by desiccation of the soil – a condition for the occurrence of the *Ranunculo-Alopecuretum* – have been encountered in the studied area. Because of the same rea-

son, no relevés of this association could be made in Ireland either (SÝKORA 1982b). The *Lolio-Potentillion* communities occurring in the studied area, the basal community of *Agrostis stolonifera*-[*Lolio-Potentillion*], the *Triglochino-Agrostietum stoloniferae,* the *Nasturtio-Alopecuretum geniculati* and the *Agrostio-Trifolietum fragiferi,* are discussed in section 4.

4. THE PLANT COMMUNITIES

4.1. Basal community of *Agrostis stolonifera*-[*Lolio-Potentillion anserinae*]. (*Table 1,* clusters 1, 2 and 4.)

As the coena presented in clusters 1, 2 and 4 cannot be assigned to one of the associations of the *Lolio-Potentillion* because character-species and sufficient differential species are lacking, they are described here as three different types of the basal community of *Agrostis stolonifera*-[*Lolio-Potentillion*]. A basal community can develop out of a coenologically saturated community under an increase of the environmental (mostly anthropogenic) dynamics resulting in the disappearance of sensitive species (KOPECKÝ & HEJNÝ 1974, 1978).

The *Eleocharis uniglumis-Carex otrubae* type (cluster 1) is characterized by the presence of *Carex otrubae* (V), *Eleocharis uniglumis* (V), *Taraxacum officinale group (IV), Festuca pratensis* (V), *Glyceria fluitans* (V), *Oenanthe fistulosa* (V) and *Bromus racemosus* (II). It has been recorded from a pasture with a soggy, heavy clay soil, irregularly grazed by horses and on a bank of a creek with a comparable soil.

The *Juncus inflexus-Carex otrubae* type (cluster 2) is characterized by the presence of *Juncus inflexus* (presence class V), *Equisetum palustre* (III), *Carex otrubae* (V), *Phragmites australis* (V) and *Mentha aquatica* (IV). It has been found on higher parts of pastures with impeded drainage, collapsed creek banks and drainage furrows, mostly on severely poached clay and in a few cases on sand.

The *Trifolium fragiferum-Carex hirta* type (cluster 4), characterized by *Carex hirta* (III) and *Trifolium fragiferum* (III) occurred in lower-lying parts of pastures, formed by the remnants of former creeks, along ditches, on the bottom of a silted-up waterway, on creek banks, in a pasture bordering a *Betuletum pubescentis* (Hueck 1929) Tüxen 1937, on the collapsed margins of pools (étangs) along the rivers of North-Western France and in drainage furrows. The severely poached, moist soil consisted of a) grey reduced sand, rich in shells and organic material, b) sandy clay, c) soft saturated, dark brown to black heavy clay, also rich in shells and organic material or d) peat. The pools along the studied rivers are the result of former excavation of peat, which explains the high content of organic material. The soil was always severely poached and in some cases the use of herbicides could be proved.

Four more types of the basal community of *Agrostis stolonifera*-[*Lolio-Potentillion*] have been described from The Netherlands and from Ireland (SÝKORA 1982a, b). In The Netherlands the *Trifolium fragiferum-Ranunculus sardous* type, characterized by *Trifolium fragiferum* (IV), *Ranunculus sardous* (III),

Juncus gerardi (III) and *Festuca arundinacea* (III) and also the *Scirpus maritimus-Juncus bufonius* type, characterized by *Scirpus maritimus* (III), occur on slightly brackish, nutrient-rich, moist soils under the disturbing influence of intensive grazing, herbicides and/or overfertilization by for instance herring-gulls, the former type being less severely disturbed than the latter.

In Ireland the *Juncus inflexus-Rumex obtusifolius* type, characterized by *Juncus inflexus* (III), *Rumex obtusifolius* (III) and *Elymus repens* (III), and the *Juncus effusus-Holcus lanatus* type, characterized by *Juncus effusus* (V) and *Holcus lanatus* (V) were found. Whereas the former is indicative for nutrient-rich, basic soils with a rather dry top soil during summer, the latter can be found on moderately acid soils with a low nutrient status and a moist top soil, even in summer.

4.2. *Triglochino-Agrostietum stoloniferae* Konczak 1968 (cluster 3), subassociation *ranunculetosum repentis*

The *Triglochino-Agrostietum stoloniferae ranunculetosum repentis* has been recorded only in extensively grazed pastures in North-Western France, in the Marais de Balançon, the Marais de Favières and in the river-valley of the Somme. In the Flemish polder area it disappeared, due to the intensification of cattle-breeding accompanied by abundant use of fertilizers. The association is restricted to unimproved pastures with a low nutrient status and is consequently very sensitive to fertilization. The character-species *Triglochin palustris* is nowadays rare to very rare in the Belgian polder area (Tanghe 1975, De Langhe et al. 1978, Van Rompaey & Delvosalle 1972). Apart from the character-species *Triglochin palustris* the association is characterized by the differential species *Juncus articulatus, Galium palustre, Ranunculus flammula, Carex nigra, Hydrocotyle vulgaris* and *Myosotis laxa* spp. *caespitosa.* In Belgium and North-Western France the last two species occur in one relevé only. *Apium nodiflorum,* a species lacking in the Dutch *Triglochino-Agrostietum,* probably because this species reaches its northern limit in The Netherlands, is present in the Belgian as well as in the Irish community with presence class III (Sýkora 1982b). The variant observed in France is differing from the Dutch and Irish variants by the high presence (IV or more) of *Juncus inflexus, Equisetum palustre, Carex hirta* and *Rumex conglomeratus.* It was found on peaty, dark brown clay. Only a few relevés were very slightly influenced by salt.

The presence of *Juncus iniflexus* (presence class IV) in the French *Triglochino-Agrostietum,* usually a community of moderately acid soils, indicates a slight calcium influence. This also may explain the low presence class of *Carex nigra* and the absence of *Hydrocotyle vulgaris* in all but one relevé. Both species belong to the *Parvocaricetea* and are indicative for acid soils. *Juncus inflexus* is a species of alkaline to subneutral soils (De Langhe et al. 1978). According to Reichgelt (1954) it grows on basic to neutral soils, whereas it has been reported as a calcicole species in Ireland (Webb 1952).

4.3. Nasturtio-Alopecuretum geniculati Sýkora 1982 (clusters 5 and 6)

Because of the presence of *Ranunculus sceleratus, Nasturtium microphyllum, Apium nodiflorum, Veronica catenata, Ranunculus sardous* and *Glyceria declinata,* the clusters 5 and 6 should be assigned to the *Nasturtio-Alopecuretum geniculati ranunculetosum scelerati* (SÝKORA 1982a). The association occurs on very soft, severely poached soils which are waterlogged throughout the year. The subassociation *ranunculetosum scelerati* is indicative for nutrient-rich, basic soils remaining very moist during the summer season. In Belgium two variants can be distinghuished: the variant with *Oenanthe fistulosa* (cluster 5) and the variant with *Juncus gerardi* (cluster 6). The variant with *Juncus gerardi,* differentiated by *Juncus gerardi, Potentilla anserina, Atriplex hastata* and *Eleocharis palustris,* is confined to more brackish soils than the variant with *Oenanthe fistulosa.* The latter is differentiated by *Oenanthe fistulosa, Lolium perenne* and *Poa trivialis.* The low presence degree of *Veronica catenata* in the variant with *Oenanthe fistulosa* and the low presence degree of *Ranunculus sardous* and *Glyceria declinata* in the variant of *Juncus gerardi* is remarkable.

Oenanthe fistulosa has its optimal occurrence in the *Nasturtio-Glycerietalia* Pignatti 1953. *Veronica catenata* is a character-species of the *Glycerio-Sparganion* Br.-Bl. & Siss. apud Boer 1942, while *Glyceria declinata* is differential for this alliance (WESTHOFF & DEN HELD 1969). I have no explanation for the alternating near absence of these species in the two variants. The variant with *Oenanthe fistulosa* was found on very soft, soaked clay along the margins of creeks. The variant with *Juncus gerardi* occurred along ditches, along creeks and drinking pools on dark brown to black, waterlogged, peaty clay mixed with shells.

4.4. *Agrostio-Triofolietum fragiferi* Sýkora 1982 (clusters 7 and 8)

From the *Agrostio-Trifolietum fragiferi,* characterized by *Trifolium fragiferum* (character-species) and *Juncus gerardi, Carex distans* and *Centaurium pulchellum,* three subassociations have been described (SÝKORA (1982a). The association is restricted to slightly brackish soils. Cluster 7 should be assigned to the subassociation *typicum* because of the presence of its differential species *Plantago major* (presence class V), *Poa trivialis* (III), *Carex otrubae* (V), *Phragmites australis* (V) and *Lotus tenuis* (IV). The subassociation has been found in a drainage furrow, along a creek and in a pasture on the bottom of an extensively grazed clay pit. The soil consisted of 10–25 cm of clay, mixed with organic material on grey reduced sand. The presence of *Juncus inflexus* (III) and *Carex flacca* (IV) is indicative for an alkaline (pH water $>$ 7) and calcium-rich soil (KRUYNE et al. 1967, OBERDORFER 1970, ELLENBERG 1978). *Carex flacca* prefers dry to moderately moist soils.

Cluster 8 can neither be assigned to the subassociation *typicum* nor to the *festucetosum rubrae.* Although *Festuca rubra* is present, the other differential species like *Holcus lanatus, Poa pratensis, Plantago coronopus, Odontites verna* ssp. *serotina, Plantago maritima, Cerastium fontanum* and *Centaurium litorale,*

are absent. Contrary to the *festucetosum rubrae, Plantago major, Lolium perenne* and *Poa trivialis* are frequent. From this and from the absence of further differentiating species it can be concluded that cluster 8 belongs to a variant of the subassociation *inops* which is less influenced by saline water than the subassociation *inops* as it has been described for The Netherlands (SÝKORA 1982a). The Dutch variant, called variant with *Eleocharis uniglumis*, occurring on the higher salt marshes, is inundated by salt water from the sea during high water spring tides and is grazed very extensively. The variant with *Poa trivialis* as recorded in Belgium, was found on a very moist soil, composed of about 8 to 15 cm of silt, mixed with organic material, on grey, reduced sand, containing shells. It occurred along a creek and was extensively grazed by horses, which explains the presence of *Festuca arundinacea* with a characteristic coverage of 2a. Because it is separated from the sea by a dyke, there is no inundation with salt water.

5. THE SYNTAXONOMICAL POSITION OF *Carex otrubae* AND *Eleocharis uniglumis*

Summarizing the data as given in the Dutch, Irish and Belgian/French tables the following can be concluded as regards *Carex otrubae* and *Eleocharis uniglumis*: *Carex otrubae* occurs with presence class III or more in the following communities: the derivate community of *Festuca arundinacea*-[*Lolio-Potentillion*], *Alopecurus* geniculatus type (presence class III); the *Agrostio-Trifolietum fragiferi typicum* (III and V); the *Triglochino-Agrostietum ranunculetosum repentis* (III) and *juncetosum gerardii* (III); the *Nasturtio-Alopecuretum geniculati ranunculetosum scelerati*, variant with *Oenanthe fistulosa* (III) and the basal community of *Agrostis stolonifera*-[*Lolio-Potentillion*], *Eleocharis uniglumis-Carex otrubae* type (V) and the *Juncus inflexus-Carex otrubae* type (V).

Like *Carex otrubae, Eleocharis uniglumis* has been found with presence class III or more in the derivate community of *Festuca arundinacea*- [*Lolio-Potentillion*], *Alopecurus geniculatus* type (III), *Nasturtio-Alopecuretum geniculati ranunculetosum scelerati* (III), *Triglochino-Agrostietum ranunculetosum repentis* (IV) and *juncetosum gerardii* (III); the *Agrostio-Trifolietum fragiferi typicum* (V) and the basal community of *Agrostis stolonifera*- [*Lolio-Potentillion*], *Eleocharis uniglumis-Carex otrubae* type (V). Besides *Eleocharis uniglumis* occurs in the *Agrostio-Trifolietum fragiferi* subassociation *inops* (IV) and in the basal community of *Agrostis stolonifera*- [*Lolio-Potentillion*], *Trifolium fragiferum-Ranunculus sardous* type. The occurrence of both species is highly correlated and I consider them to be character-species of the association group with *Eleocharis uniglumis*, further differentiated by *Phragmites australis* (see *table 1)*. The associations belonging to this group, the *Triglochino-Agrostietum stoloniferae*, the *Nasturtio-Alopecuretum geniculati* and the *Agrostio-Trifolietum fragiferi*, have a common hydrology, i.e. the top soil remains moist throughout the year. As a consequence the top soil is often rich in organic material. As *Carex*

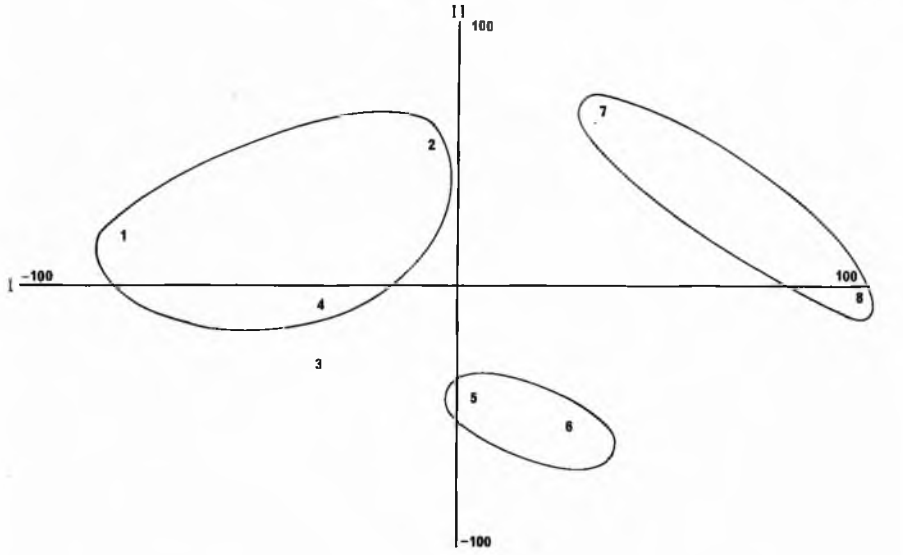

Fig. 1. Ordination diagram of the cluster centroids. Cluster numbers refer to column numbers in *table 1*.

Fig. 2. The cattle-pond is a remnant of a former creek. The poached bank is covered by the Nasturtio-Alopecuretum geniculati.

Fig. 3. The Lolio-Potentillion in the lower part of a pasture bordering a Betuletum pubescentis.

otrubae and *Eleocharis uniglumis* are salt tolerant, they both occur on fresh and on brackish soils.

6. PRINCIPAL COMPONENTS ANALYSIS

In the principal components analysis ordination of the separate relevés, the hydrological axis is clearly presented as a spiral. The production of curvilinear distortions of coenoclines is one of the disadvantages of the principal components analysis (WHITTAKER & GAUCH 1973). At the same time interpretation is difficult due to the character of the environment in which the *Lolio-Potentillion* communities have been recorded in Belgium and North-Western France. This environment, being relatively uniform, represents a mesic gradient without extreme habitats. On the other hand, ordination of the cluster centroids, i.e. the mean of the transformed cover abundance values of each species belonging to one cluster, produces axes which are clearly interpretable (*fig. 1*). Like in The Netherlands and in Ireland, the two main environmental factors are salt influence (dimension 1) and the extent to which the top soil is desiccating in summer (dimension 2). The percentage extracted variance values of these axes are respectively 31 and 20. In the basal community of *Agrostis stolonifera* (clusters 1, 2 and 4), the *Triglochino-Agrostietum stoloniferae ranunculetosum repentis* (cluster 3) and the *Nasturtio-Alopecuretum geniculati ranunculetosum scelerati* variant with *Oenanthe fistulosa* (cluster 5), the influence of salt is absent to nearly absent. The other communities occur on brackish soils with an

Fig. 4. On the bank of a former creek, poaching resulted in the formation of numerous hummocks.

increase in salt influence from the *Nasturtio-Alopecuretum ranunculetosum sce-lerati,* variant with *Juncus gerardi* (cluster 6) through the *Agrostio-Trifolietum fragiferi typicum* (cluster 7), to the *Agrostio-Trifolietum fragiferi subassociation inops* (cluster 8).

The sequence from communities on very wet soils to communities from moist soils as presented in the second axis is *Nasturtio-Alopecuretum geniculati* (cluster 5 and 6), *Triglochino-Agrostietum stoloniferae ranunculetosum repentis* (cluster 3) and the three types of the basal community of *Agrostis stolonifera* (clusters 1, 2, and 4). From the brackish communities the *Agrostio-Trifolietum fragiferi typicum* (cluster 7) was found on drier sites than the subassociation *inops* variant with *Poa trivialis* (cluster 8). Cluster 4 has actually been found to occur in the field situation as an altitudinally higher zone above clusters 5 and 6, cluster 3 has been found above cluster 6 and cluster 2 above cluster 5.

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LOLIO-POTENTILLION COMMUNITIES IN BELGIUM AND NORTH-WESTERN FRANCE

K. V. SÝKORA

Botanisch Laboratorium, Afdeling Geobotanie, Toernooiveld, 6525 ED Nijmegen

SUMMARY

The ecology and the syntaxonomy of the following Belgian and French *Lolio-Potentillion anserinae* communities are described:

1. *Ranunculo-Alopecuretum geniculati*
2. Basal community of *Agrostis stolonifera*-[*Lolio-Potentillion anserinae*]
   a) *Juncus inflexus-Carex otrubae* type
   b) *Eleocharis uniglumis-Carex otrubae* type
   c) *Trifolium fragiferum-Carex hirta* type
3. *Triglochino-Agrostietum stoloniferae ranunculetosum repentis*
4. *Nasturtio-Alopecuretum geniculati ranunculetosum scelerati*
5. *Agrostio-Trifolietum fragiferi*

a) subassociation *typicum*
b) subassociation *inops*

The syntaxonomical position of *Carex otrubae* and *Eleocharis uniglumis* is discussed, leading to the conclusion that both species are character-species of the association group with *Eleocharis uniglumis*.

The two main ecological factors are elucidated with the help of a P.C.A. ordination diagram.

1. INTRODUCTION

During June and July 1980 Belgium and North-Western France were visited in order to study the *Lolio-Potentillion anserinae* Tüxen 1947. This alliance has been separated from the *Agropyro-Rumicion cripsi* Nordhagen 1940 on floristic and ecological criteria (SÝKORA 1980). It occurs in pastures inundated during winter and spring on nutrient-rich to moderately nutrient-poor soils. The main factors responsible for the internal differentiation of the *Lolio-Potentillion* are the hydrological situation in summer, the influence of salt and the nutrient status of the soil. Communities belonging to the *Lolio-Potentillion* in The Netherlands and in Ireland have been described earlier (SÝKORA 1982a, b). For a detailed description of the synecology of this alliance I refer to these papers.

In Belgium most relevés were made along former creeks now surrounded by reclamations in the Flemish polder area. The French relevés were made on the banks of the rivers Liane, Canche, Authie and Somme, and in the Marais de Balançon and the Marais de Favières.

Eighty five percent of the Flemish polders is old or medium aged. The draining following the reclamation (7th, 8th, 11th and 12th century) caused compaction of the peat and as a consequence the soil level was lowered considerably. This worsened the drainage situation, so that the polders can be utilized as pastures only. After the reclamation the existing creeks and their branches were

used as a basis for the drainage system. The resulting sinuous drains are easily obstructed; besides they are shallow, making drainage less efficient (VANHECKE 1977). Fluctuations of the water-level with 50 cm or more, the high nutrient status of the soil and the presence of cattle explain the frequent occurrence of the *Lolio-Potentillion* along the Flemish creeks. The water of these creeks is sometimes brackish due to the presence of late Atlantic and Subboreal saliferous peat layers on a depth of 1–5 m below Ordnance Datum and the seepage of salt-containing ground water. The salt enrichment of the peat was caused by inundation of it with sea water during transgressions of the sea in the early part of the christian era (DE RIDDER 1957, VISSCHER 1975, BIJHOUWER 1977, BRAND 1978, GUERLESQUIN & WATTEZ (1979), ANONYMUS (1979). The moist grasslands along the creeks have a high ornithological significance (BECUWE 1977, HOUWEN 1977, ANONYMUS 1979).

Because of the hilly character of North-Western France the *Lolio-Potentillion* is restricted to the riversides and the marshes near the mouth of the rivers. The rivers in this area are running from south-east to north-west. As a consequence of the relative shortness of these rivers, the small size of the watersheds and the artificially improved discharge, water fluctuations are considerably less pronounced than in the river-bed of, for instance, the Rhine and the Waal.

As an important part of the riversides are either well drained or ungrazed (resulting in extensive reed-swamps used for shooting water-fowl) the *Lolio-Potentillion* is well developed only locally, for instance along ponds resulting from the cutting of peat, along ditches and drainage furrows and in low lying parts of pastures with impeded drainage. The presence of *Lolio-Potentillion* communities in North-Western France has been previously recorded by GÉHU (1961), GÉHU & WATTEZ (1965), FRILEUX & GÉHU (1975), WATTEZ (1967, 1975), FRILEUX (1976) and BOURNERIAS et al. 1976.

The vegetation of humid grasslands inclusive the *Lolio-Potentillion* has been severely degraded by drainage, intensification of agricultural practices e.g., use of herbicides, overfertilization, overstocking with cattle, termination of grazing, the planting of poplars, the canalization of the rivers and industrialization (WATTEZ 1975, FRILEUX & GÉHU 1975, FRILEUX 1976).

2. METHODS

The methods were the same as described in SÝKORA 1982b (this issue, p. 189)

3. STATUS OF THE ALLIANCE IN BELGIUM AND NORTH-WESTERN FRANCE.

In Western Germany and The Netherlands the most characteristic and best developed association of the *Lolio-Potentillion* is the *Ranunculo-Alopecuretum geniculati*. It is the first association which has been described and it can be considered as the 'type-association' of the alliance. However, none of the communities presented in this paper can be assigned to the *Ranunculo-Alopecuretum*. Only *Carex hirta* (character-species for this association), *Equisetum palustre*

Table 1. Synoptic table of the *Lolio-Potentillion* communities studied in Belgium and North-Western France. In the first column of every cluster the presence class is given (+ = present only in one relevé; I = 1–20%; II = 21–40%; III = 41–60%; IV = 61–80%; V = 81–100%).

In the second column the characteristic coverage is given according to the Braun-Blanquet scale as refined by BARKMAN et al. (1964).

Communities: clusters 1, 2 and 4: Basal community of Agrostis stolonifera-[Lolio-Potentillion anserinae], Eleocharis uniglumis-Carex otrubae type (cluster 1); Juncus inflexus-Carex otrubae type (cluster 2); Trifolium fragiferum-Carex hirta type (cluster 4). Triglochino-Agrostietum stoloniferae ranunculetosum repentis (cluster 3).

clusters 5 and 6: Nasturtio-Alopecuretum geniculati ranunculetosum sceleratí, variant with Oenanthe fistulosa (cluster 5) and variant with Juncus gerardi (cluster 6).

clusters 7 and 8: Agrostio-Trifolietum fragiferi, subass. typicum (cluster 7) and subass. inops, variant with Poa trivialis (cluster 8).

cluster number	1		2		3		4		5		6		7		8	
number of relevés	6		12		20		52		15		20		7		5	
Plantaginetea + Lolio-Plantaginetum character-species																
Potentilla anserina	+	2m	V	2m	IV	2m	IV	1	II	1	V	1	III	2m	III	1
Plantago major	III	+	II	+	III	+	IV	+	IV	+	IV	1	V	1	IV	1
Lolium perenne			II	+	II	+	III	1	III	1	I	+	III	+	IV	1
Poa annua							I	1								
Polygonum aviculare			I	+			I	+			I	+				
Lolio-Potentillion, character-species + constant companion																
Agrostis stolonifera	V	2b	V	3	V	3	V	3	V	3	V	3	V	3	V	3
c.c. Poa trivialis	V	2b	IV	2a	IV	2a	V	2b	V	2m	II	2m	III	1	V	1
Alopecurus geniculatus	V	2m	III	1	V	2b	V	2a	V	2b	V	2b	IV	1		
Rumex crispus	V	+	III	+	II	+	III	+	II	+	III	+	III	+	+	+
Juncus inflexus			V	2a	IV	1	II	+	II	2m			III	1		
Ranunculo-Alopecuretum, character- and differential species																
Taraxacum officinale group	IV	1	I	+	I	+	I	+					+	+	+	+
Equisetum palustre			III	+	III	1	I	1					+	+		
Carex hirta			I	2m	IV	1	III	1	I	1	I	2m				
Elymus repens	II	1	I	1			I	1			II	1	+	+		
Lysimachia nummularia			II	1	I	+	I	1	+	1	I	+				
Polygonum amphibium			II	1	II	1	I	1								
Potentilla reptans	+	+	I	1			+	+								
Rorippa amphibia							+	+			+	+				
Phalaris arundinacea							I	+								
Myosotis scorpioides							I	1								
Glyceria maxima							I	1								
Association group with Eleocharis uniglumis; character- and differential species.																
Carex otrubae	V	+	V	1	III	+	II	+	III	1	II	+	V	1	+	+
Phragmites australis	III	2m	V	1	I	1	II	1	III	1	II	1	V	2m		
Eleocharis uniglumis	V	2a	II	2a	+	1	I	2m	+	1	II	1	+	1		
Triglochino-Agrostietum, character- and differential species																
Juncus articulatus	III	1	III	+	V	1	III	1	II	1	II	1	V	2m	+	+
Galium palustre	II	+	IV	+	III	+	III	1	+	+	I	+				
Triglochin palustris			+	1	III	1	I	1	II	1	III	2m			III	1
Ranunculus flammula					III	1	I	1								
Carex nigra					II	1	+	2a								
Hydrocotyle vulgaris					+	1	I	1			II	1				
Myosotis laxa ssp. caespitosa	+	+	+	+	+	+	II	1	I	+						
Nasturtio-Alopecuretum																
Ranunculus sceleratus			+	+			II	+	III	+	III	+	+	+	II	1
Nasturtium microphyllum			II	+	I	1	II	+	II	+	IV	1			+	+
Apium nodiflorum			+	+	III	1	II	1	II	1	III	1	II	+	+	+
Veronica catenata					I	1	I	+	+	+	III	+	II	+		
Ranunculus sardous			I	+	I	+	I	+	III	1	+	1				
Glyceria declinata			+	1	II	1	II	1	III	1	I	1				
Epilobium parviflorum			+	+	II	+	II	+			I	+	II	1		
Agrostio-Trifolietum fragiferi																
Trifolium fragiferum	+	2m	I	1	IV	2m	III	1	IV	1	III	1	V	1	V	2m
Juncus gerardi			I	2m	II	1	I	1	I	2m	IV	1	V	2m	IV	2a
Carex distans					II	+							III	2m	IV	1
Lotus tenuis					II	1							IV	+		
Centaurium pulchellum													II	+		

cluster number	1	2	3	4	5	6	7	8
Glaux maritima					I 1	+ 1		III 2m
Festuca rubra		+ 1	I 1					III 2m
Triglochin maritima								+ +
Further differentiation								
Festuca pratensis	V 1	I +	II +	I +	+ +	+ +		
Glyceria fluitans	V 1	II 1	II 1	II 1		I 2m	II +	
Oenanthe fistulosa	V 1	+ 1	II +	II 1	III 1	I +	+ +	
Bromus racemosus	II +							
Cardamine pratensis	IV 1	III +	IV 1	I +				
Carex disticha			II 1					
Bellis perennis			I +	I +	+ +		V 1	
Carex flacca				I 1			IV 1	
Pulicaria dysenterica		II 1	II +	I +			IV +	
Leontodon autumnalis			+ +	I +			III +	
Salix repens							III +	
Festuca arundinacea	+ +	+ +	+ +	+ +				V 2a
Companion species								
Ranunculus repens	V 2a	V 1	V 2a	V 2a	IV 1	III 1	IV 1	+ +
Trifolium repens	IV 2m	III 1	I 1	V 1	II 1	II +	IV 1	IV 2m
Juncus bufonius group	+ 1	+ 1	I 2m	II 1	II 1	II 1	III 1	II 1
Drepanocladus aduncus	III 2a	+ +	III 2a	I +	I +	I 1	V 2m	+ 1
Mentha aquatica		IV 1	III +	III 1	I +	I 2m	V 1	+ +
Rumex conglomeratus	+ +	III +	III +	II +	I 1	I 1		
Scirpus maritimus		I 1	I 2m	I 1	II 1	III 1		IV 1
Cerastium fontanum	+ +		I +	II +	+ +		+ +	
Holcus lanatus	III 1	II +	II +	II 1				+ +
Eleocharis palustris		I 1	III 2m	II 2m		III 2m	I 1	
Atriplex hastata				I 1	I +	III 1		II +
Equisetum arvense		+ +	I +	+ +			II 1	
Phleum pratense	II +		I 1	I +		+ +		
Senecio aquaticus		+ +	II +	I +		+ +		
Odontites verna ssp. serotina		II 1	I +	I 1				
Veronica beccabunga			I 1	II +	+ +			
Brachythecium rutabulum	III 1			I +				
Calliergonella cuspidata			II +	I 1				
Chenopodium rubrum				I +	II +	II 1		

Species with presence class I or +: Alisma plantago-aquatica (cluster number 6), Arrhenatherum elatius (2), Aster tripolium (4, 6, 8), Atriplex patula (4), Berula erecta (2, 4), Bidens cernua (4), Bidens tripartita (6, 4), Carex acutiformis (4), Carex riparia (5, 4), Catabrosa aquatica (4), Cirsium arvense (2, 6, 4, 1), Cynosurus cristatus (4), Epilobium hirsutum (2), Epilobium obscurum (3), Epilobium palustre (2), Equisetum fluviatile (4), Filipendula ulmaria (4, 3), Hippuris vulgaris (4, 6), Hordeum secalinum (5, 6, 4), Iris pseudacorus (2, 4), Juncus acutiflorus (4), Juncus effusus (4), Lychnis flos-cuculi (4), Lycopus europaeus (2, 6, 3), Lythrum salicaria (7, 6), Medicago lupulina (6), Myosoton aquaticum (4), Oenanthe aquatica (5, 7, 6, 4), Poa pratensis (8), Polygonum hydropiper (4), Polygonum mite (2, 6, 4, 3), Prunella vulgaris (4, 3), Puccinellia distans (6, 4), Ranunculus acris (4, 3), Rhynchostegiella curviseta (4), Rumex obtusifolius (4), Rumex palustris (5, 6), Sagina procumbens (4), Samolus valerandi (2, 6, 4, 8), Scirpus lacustris ssp. tabernaemontani (5, 6, 4, 3), Scirpus setaceus (4), Solanum dulcamara (2, 4), Spergularia marina (6), Stellaria alsine (4), Stellaria media (2, 4), Symphytum officinale (6, 4), Trifolium pratense (2, 4), Urtica dioica (2, 4).

and *Taraxacum officinale* group (differential species) are present with presence class III or more. The character-species *Potentilla reptans, Rorippa sylvestris, Juncus compressus, Inula britannica, Mentha pulegium* and the differential species *Phalaris arundinacea, Polygonum amphibium, Elymus repens, Lysimachia nummularia, Myosotis scorpioides, Rorippa amphibia, Alopecurus pratensis, Glechoma hederacea* and *Glyceria maxima* are absent or are present with presence class II or less.

The ecological explanation for this phenomenon can be found in the hydrology of the Flemish creeks and the French riversides. Because of insufficient fluctuation of the water-level, no sites with prolonged inundation followed by desiccation of the soil – a condition for the occurrence of the *Ranunculo-Alopecuretum* – have been encountered in the studied area. Because of the same rea-

son, no relevés of this association could be made in Ireland either (SÝKORA 1982b). The *Lolio-Potentillion* communities occurring in the studied area, the basal community of *Agrostis stolonifera*-[*Lolio-Potentillion*], the *Triglochino-Agrostietum stoloniferae*, the *Nasturtio-Alopecuretum geniculati* and the *Agrostio-Trifolietum fragiferi*, are discussed in section 4.

4. THE PLANT COMMUNITIES

4.1. Basal community of *Agrostis stolonifera*-[*Lolio-Potentillion anserinae*]. (*Table 1*, clusters 1, 2 and 4.)

As the coena presented in clusters 1, 2 and 4 cannot be assigned to one of the associations of the *Lolio-Potentillion* because character-species and sufficient differential species are lacking, they are described here as three different types of the basal community of *Agrostis stolonifera*-[*Lolio-Potentillion*]. A basal community can develop out of a coenologically saturated community under an increase of the environmental (mostly anthropogenic) dynamics resulting in the disappearance of sensitive species (KOPECKÝ & HEJNÝ 1974, 1978).

The *Eleocharis uniglumis-Carex otrubae* type (cluster 1) is characterized by the presence of *Carex otrubae* (V), *Eleocharis uniglumis* (V), *Taraxacum officinale group (IV)*, *Festuca pratensis* (V), *Glyceria fluitans* (V), *Oenanthe fistulosa* (V) and *Bromus racemosus* (II). It has been recorded from a pasture with a soggy, heavy clay soil, irregularly grazed by horses and on a bank of a creek with a comparable soil.

The *Juncus inflexus-Carex otrubae* type (cluster 2) is characterized by the presence of *Juncus inflexus* (presence class V), *Equisetum palustre* (III), *Carex otrubae* (V), *Phragmites australis* (V) and *Mentha aquatica* (IV). It has been found on higher parts of pastures with impeded drainage, collapsed creek banks and drainage furrows, mostly on severely poached clay and in a few cases on sand.

The *Trifolium fragiferum-Carex hirta* type (cluster 4), characterized by *Carex hirta* (III) and *Trifolium fragiferum* (III) occurred in lower-lying parts of pastures, formed by the remnants of former creeks, along ditches, on the bottom of a silted-up waterway, on creek banks, in a pasture bordering a *Betuletum pubescentis* (Hueck 1929) Tüxen 1937, on the collapsed margins of pools (étangs) along the rivers of North-Western France and in drainage furrows. The severely poached, moist soil consisted of a) grey reduced sand, rich in shells and organic material, b) sandy clay, c) soft saturated, dark brown to black heavy clay, also rich in shells and organic material or d) peat. The pools along the studied rivers are the result of former excavation of peat, which explains the high content of organic material. The soil was always severely poached and in some cases the use of herbicides could be proved.

Four more types of the basal community of *Agrostis stolonifera*-[*Lolio-Potentillion*] have been described from The Netherlands and from Ireland (SÝKORA 1982a, b). In The Netherlands the *Trifolium fragiferum-Ranunculus sardous* type, characterized by *Trifolium fragiferum* (IV), *Ranunculus sardous* (III),

Juncus gerardi (III) and *Festuca arundinacea* (III) and also the *Scirpus maritimus-Juncus bufonius* type, characterized by *Scirpus maritimus* (III), occur on slightly brackish, nutrient-rich, moist soils under the disturbing influence of intensive grazing, herbicides and/or overfertilization by for instance herring-gulls, the former type being less severely disturbed than the latter.

In Ireland the *Juncus inflexus-Rumex obtusifolius* type, characterized by *Juncus inflexus* (III), *Rumex obtusifolius* (III) and *Elymus repens* (III), and the *Juncus effusus-Holcus lanatus* type, characterized by *Juncus effusus* (V) and *Holcus lanatus* (V) were found. Whereas the former is indicative for nutrient-rich, basic soils with a rather dry top soil during summer, the latter can be found on moderately acid soils with a low nutrient status and a moist top soil, even in summer.

4.2. *Triglochino-Agrostietum stoloniferae* Konczak 1968 (cluster 3), subassociation *ranunculetosum repentis*

The *Triglochino-Agrostietum stoloniferae ranunculetosum repentis* has been recorded only in extensively grazed pastures in North-Western France, in the Marais de Balançon, the Marais de Favières and in the river-valley of the Somme. In the Flemish polder area it disappeared, due to the intensification of cattle-breeding accompanied by abundant use of fertilizers. The association is restricted to unimproved pastures with a low nutrient status and is consequently very sensitive to fertilization. The character-species *Triglochin palustris* is nowadays rare to very rare in the Belgian polder area (TANGHE 1975, DE LANGHE et al. 1978, VAN ROMPAEY & DELVOSALLE 1972). Apart from the character-species *Triglochin palustris* the association is characterized by the differential species *Juncus articulatus, Galium palustre, Ranunculus flammula, Carex nigra, Hydrocotyle vulgaris* and *Myosotis laxa* spp. *caespitosa.* In Belgium and North-Western France the last two species occur in one relevé only. *Apium nodiflorum,* a species lacking in the Dutch *Triglochino-Agrostietum,* probably because this species reaches its northern limit in The Netherlands, is present in the Belgian as well as in the Irish community with presence class III (SÝKORA 1982b). The variant observed in France is differing from the Dutch and Irish variants by the high presence (IV or more) of *Juncus inflexus, Equisetum palustre, Carex hirta* and *Rumex conglomeratus.* It was found on peaty, dark brown clay. Only a few relevés were very slightly influenced by salt.

The presence of *Juncus inflexus* (presence class IV) in the French *Triglochino-Agrostietum,* usually a community of moderately acid soils, indicates a slight calcium influence. This also may explain the low presence class of *Carex nigra* and the absence of *Hydrocotyle vulgaris* in all but one relevé. Both species belong to the *Parvocaricetea* and are indicative for acid soils. *Juncus inflexus* is a species of alkaline to subneutral soils (DE LANGHE et al. 1978). According to REICHGELT (1954) it grows on basic to neutral soils, whereas it has been reported as a calcicole species in Ireland (WEBB 1952).

4.3. Nasturtio-Alopecuretum geniculati Sýkora 1982 (clusters 5 and 6)

Because of the presence of *Ranunculus sceleratus, Nasturtium microphyllum, Apium nodiflorum, Veronica catenata, Ranunculus sardous* and *Glyceria declinata,* the clusters 5 and 6 should be assigned to the *Nasturtio-Alopecuretum geniculati ranunculetosum scelerati* (SÝKORA 1982a). The association occurs on very soft, severely poached soils which are waterlogged throughout the year. The subassociation *ranunculetosum scelerati* is indicative for nutrient-rich, basic soils remaining very moist during the summer season. In Belgium two variants can be distinghuished: the variant with *Oenanthe fistulosa* (cluster 5) and the variant with *Juncus gerardi* (cluster 6). The variant with *Juncus gerardi,* differentiated by *Juncus gerardi, Potentilla anserina, Atriplex hastata* and *Eleocharis palustris,* is confined to more brackish soils than the variant with *Oenanthe fistulosa.* The latter is differentiated by *Oenanthe fistulosa, Lolium perenne* and *Poa trivialis.* The low presence degree of *Veronica catenata* in the variant with *Oenanthe fistulosa* and the low presence degree of *Ranunculus sardous* and *Glyceria declinata* in the variant of *Juncus gerardi* is remarkable.

Oenanthe fistulosa has its optimal occurrence in the *Nasturtio-Glycerietalia* Pignatti 1953. *Veronica catenata* is a character-species of the *Glycerio-Sparganion* Br.-Bl. & Siss. apud Boer 1942, while *Glyceria declinata* is differential for this alliance (WESTHOFF & DEN HELD 1969). I have no explanation for the alternating near absence of these species in the two variants. The variant with *Oenanthe fistulosa* was found on very soft, soaked clay along the margins of creeks. The variant with *Juncus gerardi* occurred along ditches, along creeks and drinking pools on dark brown to black, waterlogged, peaty clay mixed with shells.

4.4. *Agrostio-Triofolietum fragiferi* Sýkora 1982 (clusters 7 and 8)

From the *Agrostio-Trifolietum fragiferi,* characterized by *Trifolium fragiferum* (character-species) and *Juncus gerardi, Carex distans* and *Centaurium pulchellum,* three subassociations have been described (SÝKORA (1982a). The association is restricted to slightly brackish soils. Cluster 7 should be assigned to the subassociation *typicum* because of the presence of its differential species *Plantago major* (presence class V), *Poa trivialis* (III), *Carex otrubae* (V), *Phragmites australis* (V) and *Lotus tenuis* (IV). The subassociation has been found in a drainage furrow, along a creek and in a pasture on the bottom of an extensively grazed clay pit. The soil consisted of 10–25 cm of clay, mixed with organic material on grey reduced sand. The presence of *Juncus inflexus* (III) and *Carex flacca* (IV) is indicative for an alkaline (pH water $>$ 7) and calcium-rich soil (KRUYNE et al. 1967, OBERDORFER 1970, ELLENBERG 1978). *Carex flacca* prefers dry to moderately moist soils.

Cluster 8 can neither be assigned to the subassociation *typicum* nor to the *festucetosum rubrae.* Although *Festuca rubra* is present, the other differential species like *Holcus lanatus, Poa pratensis, Plantago coronopus, Odontites verna* ssp. *serotina, Plantago maritima, Cerastium fontanum* and *Centaurium litorale,*

are absent. Contrary to the *festucetosum rubrae, Plantago major, Lolium perenne* and *Poa trivialis* are frequent. From this and from the absence of further differentiating species it can be concluded that cluster 8 belongs to a variant of the subassociation *inops* which is less influenced by saline water than the subassociation *inops* as it has been described for The Netherlands (SÝKORA 1982a). The Dutch variant, called variant with *Eleocharis uniglumis,* occurring on the higher salt marshes, is inundated by salt water from the sea during high water spring tides and is grazed very extensively. The variant with *Poa trivialis* as recorded in Belgium, was found on a very moist soil, composed of about 8 to 15 cm of silt, mixed with organic material, on grey, reduced sand, containing shells. It occurred along a creek and was extensively grazed by horses, which explains the presence of *Festuca arundinacea* with a characteristic coverage of 2a. Because it is separated from the sea by a dyke, there is no inundation with salt water.

5. THE SYNTAXONOMICAL POSITION OF *Carex otrubae* AND *Eleocharis uniglumis*

Summarizing the data as given in the Dutch, Irish and Belgian/French tables the following can be concluded as regards *Carex otrubae* and *Eleocharis uniglumis*: *Carex otrubae* occurs with presence class III or more in the following communities: the derivate community of *Festuca arundinacea*-[*Lolio-Potentillion*], *Alopecurus* geniculatus type (presence class III); the *Agrostio-Trifolietum fragiferi typicum* (III and V); the *Triglochino-Agrostietum ranunculetosum repentis* (III) and *juncetosum gerardii* (III); the *Nasturtio-Alopecuretum geniculati ranunculetosum scelerati,* variant with *Oenanthe fistulosa* (III) and the basal community of *Agrostis stolonifera*-[*Lolio-Potentillion*], *Eleocharis uniglumis-Carex otrubae* type (V) and the *Juncus inflexus-Carex otrubae* type (V).

Like *Carex otrubae, Eleocharis uniglumis* has been found with presence class III or more in the derivate community of *Festuca arundinacea-* [*Lolio-Potentillion*], *Alopecurus geniculatus* type (III), *Nasturtio-Alopecuretum geniculati ranunculetosum scelerati* (III), *Triglochino-Agrostietum ranunculetosum repentis* (IV) and *juncetosum gerardii* (III); the *Agrostio-Trifolietum fragiferi typicum* (V) and the basal community of *Agrostis stolonifera-* [*Lolio-Potentillion*], *Eleocharis uniglumis-Carex otrubae* type (V). Besides *Eleocharis uniglumis* occurs in the *Agrostio-Trifolietum fragiferi* subassociation *inops* (IV) and in the basal community of *Agrostis stolonifera-* [*Lolio-Potentillion*], *Trifolium fragiferum-Ranunculus sardous* type. The occurrence of both species is highly correlated and I consider them to be character-species of the association group with *Eleocharis uniglumis,* further differentiated by *Phragmites australis* (see *table 1).* The associations belonging to this group, the *Triglochino-Agrostietum stoloniferae,* the *Nasturtio-Alopecuretum geniculati* and the *Agrostio-Trifolietum fragiferi,* have a common hydrology, i.e. the top soil remains moist throughout the year. As a consequence the top soil is often rich in organic material. As *Carex*

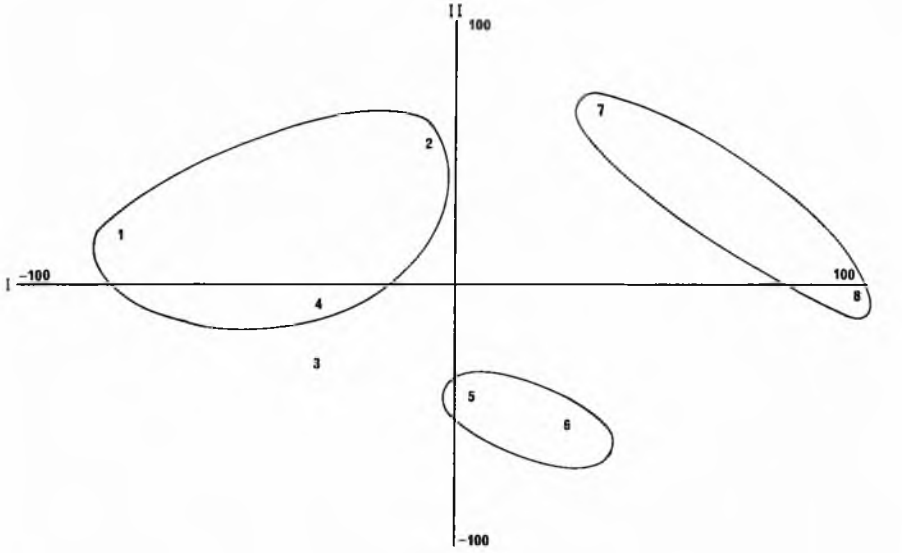

Fig. 1. Ordination diagram of the cluster centroids. Cluster numbers refer to column numbers in *table 1*.

Fig. 2. The cattle-pond is a remnant of a former creek. The poached bank is covered by the Nasturtio-Alopecuretum geniculati.

Fig. 3. The Lolio-Potentillion in the lower part of a pasture bordering a Betuletum pubescentis.

otrubae and *Eleocharis uniglumis* are salt tolerant, they both occur on fresh and on brackish soils.

6. PRINCIPAL COMPONENTS ANALYSIS

In the principal components analysis ordination of the separate relevés, the hydrological axis is clearly presented as a spiral. The production of curvilinear distortions of coenoclines is one of the disadvantages of the principal components analysis (WHITTAKER & GAUCH 1973). At the same time interpretation is difficult due to the character of the environment in which the *Lolio-Potentillion* communities have been recorded in Belgium and North-Western France. This environment, being relatively uniform, represents a mesic gradient without extreme habitats. On the other hand, ordination of the cluster centroids, i.e. the mean of the transformed cover abundance values of each species belonging to one cluster, produces axes which are clearly interpretable (*fig. 1*). Like in The Netherlands and in Ireland, the two main environmental factors are salt influence (dimension 1) and the extent to which the top soil is desiccating in summer (dimension 2). The percentage extracted variance values of these axes are respectively 31 and 20. In the basal community of *Agrostis stolonifera* (clusters 1, 2 and 4), the *Triglochino-Agrostietum stoloniferae ranunculetosum repentis* (cluster 3) and the *Nasturtio-Alopecuretum geniculati ranunculetosum scelerati* variant with *Oenanthe fistulosa* (cluster 5), the influence of salt is absent to nearly absent. The other communities occur on brackish soils with an

Fig. 4. On the bank of a former creek, poaching resulted in the formation of numerous hummocks.

increase in salt influence from the *Nasturtio-Alopecuretum ranunculetosum scelerati,* variant with *Juncus gerardi* (cluster 6) through the *Agrostio-Trifolietum fragiferi typicum* (cluster 7), to the *Agrostio-Trifolietum fragiferi subassociation inops* (cluster 8).

The sequence from communities on very wet soils to communities from moist soils as presented in the second axis is *Nasturtio-Alopecuretum geniculati* (cluster 5 and 6), *Triglochino-Agrostietum stoloniferae ranunculetosum repentis* (cluster 3) and the three types of the basal community of *Agrostis stolonifera* (clusters 1, 2, and 4). From the brackish communities the *Agrostio-Trifolietum fragiferi typicum* (cluster 7) was found on drier sites than the subassociation *inops* variant with *Poa trivialis* (cluster 8). Cluster 4 has actually been found to occur in the field situation as an altitudinally higher zone above clusters 5 and 6, cluster 3 has been found above cluster 6 and cluster 2 above cluster 5.

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SYNTAXONOMIC STATUS OF THE JUNCO-MENTHETUM LONGIFOLIAE LOHMEYER 1953, THE JUNCO-MENTHETUM ROTUNDIFOLIAE OBERDORFER (1952) 1957 AND THE CARICETUM VULPINAE NOWINSKI 1927

K. V. SÝKORA

Botanisch Laboratorium, Afdeling Geobotanie, Toernooiveld, 6525 ED Nijmegen

SUMMARY

A survey is given of the syntaxonomic status and the internal differentiation of the *Junco-Menthetum longifoliae* (and *rotundifoliae*) and the *Caricetum vulpinae* in Europe. The following conclusions can be drawn:

A. *Junco-Menthetum longifoliae*

1. Vegetation stands containing *Mentha longifolia* do not belong to one association but are conglomerates i.e. mixtures of fragments.
2. *Mentha longifolia* is not characteristic of the *Lolio-Potentillion* but its epharmony is comparable to that of the *Filipendulion* species. The tall-forb character of the conglomerates is conspicuous.
3. The *Plantaginetea* element is of only minor importance under extensive grazing but increases with intensification of this factor.

B. *Junco-Menthetum rotundifoliae*

1. The status of this association as a separate association is insufficiently founded.

C. *Caricetum vulpinae* Tüxen 1947

1. Contrary to the suggestion of WESTHOFF & VAN LEEUWEN (1966) and WESTHOFF & DEN HELD (1969), *Carex vulpina* is not a character species of the *Lolio-Potentillion*. The preponderance of *Magnocaricion* and *Phragmitetea* species justifies the assignment of the *Caricetum vulpinae* to these syntaxa.
2. On a European scale no subassociations can be distinguished.
3. The main internal differentiation is expressed by a gradual increase of the weight of the *Molinio-Arrhenatheretea* and the *Scheuchzerio-Caricetea* species as the dynamics of the hydrology decreases.

1. INTRODUCTION

In previous papers (SÝKORA 1980, 1982a, 1982b, 1982c) the syntaxonomy and synecology of the *Lolio-Potentillion anserinae* Tx. 1947 in the northern part of the Atlantic domain have been discussed. In this paper a survey is given of the *Junco-Menthetum longifoliae* Lohmeyer 1953 and the *Caricetum vulpinae* Nowinsky 1927. Furthermore the syntaxonomic position of the *Junco-Menthetum rotundifoliae* Oberdorfer 1952 is discussed. The first community is usually considered to belong to the *Agropyro-Rumicion crispi* Nordh. 1940 em. Tx. 1950, the alliance in which Tüxen combined the communities occurring on organic

drift material along the coasts of the northern part of Europe (*Agropyro-Rumicion crispi* Nordh. 1940) with communities from inundated pastures (*Lolio-Potentillion anserinae* Tx. 1947). According to Sýkora (1980) this combination is unjustified, however.

According to LIPPERT (1966) and CREDARO & PIROLA (1975), the systematic position of the *Junco-Menthetum longifoliae* is unclear and of dubious interpretation. From the *Junco-Menthetum rotundifoliae* only very few relevés have been published (RUNGE 1980, TÜXEN 1976). In structural and chorological respect as well as in its floristic assemblage, this community has much resemblance to the *Junco-Menthetum longifoliae; Mentha longifolia* and *Mentha rotundifolia* are epharmonically closely related.

WESTHOFF & VAN LEEUWEN (1966) suggested that *Carex vulpina* is a characteristic species of the *Agropyro-Rumicion crispi*. In 1969 WESTHOFF & DEN HELD classified the *Caricetum vulpinae* into this alliance. Other authors, however, consider it a *Magnocaricion* community (tall sedge communities).

2. METHODS

In the relevant literature both separate relevés and synoptic tables of the *Junco-Menthetum* and the *Caricetum vulpinae* have been published. For the construction of *tables 1* and *5*, 68 *Junco-Menthetum* and 96 *Caricetum vulpinae* relevés were gathered from literature, mentioned in chapter 3 and on p. 413.

The rough tables were structured by means of the Tabord program (VAN DER MAAREL et al. 1978, VAN DER MAAREL 1979), using similarity ratio (WISHART 1969) to measure similarities between relevés and clusters. After summarizing the results in synoptic tables the synoptic clusters as presented in the literature were added. The final tables represent a total of 91 relevés of the *Junco-Menthetum longifoliae* (inclusive the *Junco-Menthetum rotundifoliae* with 11 relevés) and about 194 relevés of the Caricetum vulpinae. In order to determine the importance of the phytosociological elements in each column the systematic group value was calculated (TÜXEN & ELLENBERG 1937), for which I used the formula

$$Dx = Gx^2 \cdot 100/t.n$$

in which Dx = the systematic group value for species group x, Gx^2 = the squared sum of the presence class values for all species forming part of a group x, t = the sum of all presence class values of all species in the column under consideration and n = total number of species in species group x. Thus the proportion of the species group is multiplied by the average presence class value in order to diminish the effect of the species with low presence class values. The more accidental species with a low presence occur in the column, the lower the systematic group value will be. The systematic group values of the *Junco-Menthetum longifoliae,* the *Junco-Menthetum rotundifoliae* and the *Caricetum vulpinae* are presented in *tables 2* and *3*. The phytosociologic status of each species was determined from OBERDORFER (1979), ELLENBERG (1978), WESTHOFF & DEN HELD (1969) and SÝKORA (1982a, b and c).

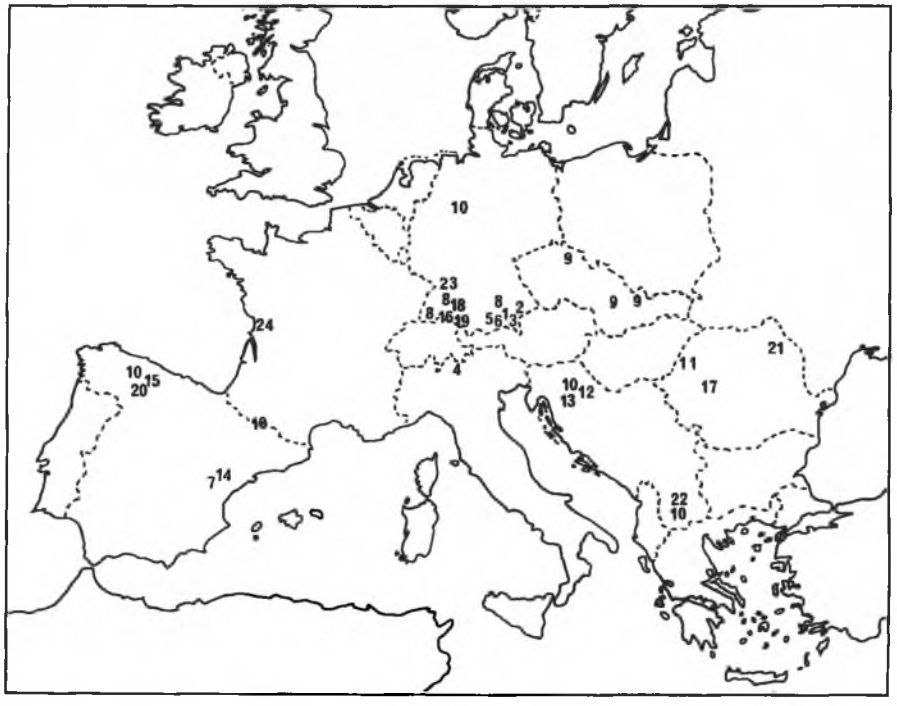

Fig. 1. Distribution of the conglomerates of *Mentha longifolia*. Numbers on the map correspond with the column numbers in *table 1*.

For a principal components ordination of the *Caricetum vulpinae* (*fig. 3*) I used the Ordina Program (ROSKAM 1971). In this analysis the presence class values of the species in each column were used. The localities of the relevés on which the *tables 1* and *5* are based, are indicated in *figs. 1* and *2*.

Species nomenclature follows Flora Europaea (TUTIN et al. 1964–1980) for phanerogams and LANDWEHR (1966) for bryophytes.

3. MIXTUM COMPOSITUM OF MENTHA LONGIFOLIA *(table 1)*

3.1. *Table 1* in which the *Junco-Menthetum* communities gathered from literature have been combined, is markedly heterogeneous. The floristic composition of the columns is very distinct. Based on these results I conclude that a *Juncus inflexus-Mentha longifolia* association as a unit does not exist, and that the combination of local units containing *Mentha longifolia* is a mixtum compositum. This position will be elucidated in the following sections. In the table structured by means of the Tabord Program, only few relevés have been relocated. The only cluster composed of relevés from different localities (different papers) is cluster 10, a combination of relevés from Germany, Jugoslavia and Spain. As

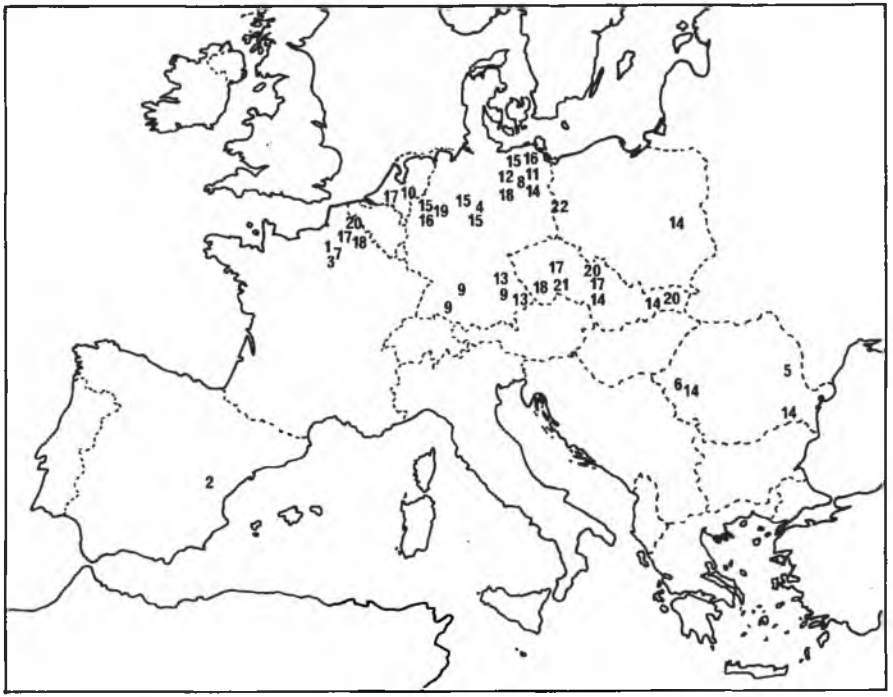

Fig. 2. Distribution of the *Caricetum vulpinae*.
Numbers on the map correspond with the column numbers in *table 5*.

the separate columns represent mixtures of fragments i.e. mixtures of communities that lack sufficient diagnostic species to be able to describe them as associations, the term conglomerate (devised by Westhoff, personal communication) has been introduced in this paper.

3.1.1. Conglomerate of Mentha longifolia and Rumex alpinus (columns 1, 2 and 3)

The conglomerate of *Mentha longifolia* and *Rumex alpinus* refers to a tall forb vegetation floristically forming a transition between the *Molinio-Arrhenatheretea* Tx. 1937 and the *Rumicion alpini* (Rübel 1933) Klika 1944. The *Molinio-Arrhenatheretea* species have the greatest systematic group value, followed by the *Artemisietea vulgaris (table 2)*. In this conglomerate the species of the Plantaginetea are of minor importance only. The conglomerate is differentiated by the *Molinio-Arrhenatheretea* species *Chaerophyllum hirsutum, Carum carvi, Veronica chamaedrys, Alchemilla xanthochlora* and *Poa alpina. Chaerophyllum hirsutum* is a character species of the *Chaerophyllo-Ranunculetum aconitifolii* Oberd. 1952, a montane association belonging to the *Calthion palustris* Tx. 1936 and occurring in meadows along swiftly running water. It is also frequent in tall forb communities of the *Filipendulion* (RUNGE 1980, OBERDORFER 1979).

Other differential species such as *Lamium maculatum*, *Rumex alpinus* and *Veratrum album* belong to the *Artemisietea*. *Veratrum album* and *Rumex alpinus* have their optimal occurrence in the strongly nitrophilic *Rumicetum alpini* Beg. 1922. This association forms a tall forb community occurring everywhere in the Alps between 900 and 2640 m near shepherd's huts where dung hills have been cast, liquid manure is seeping or where rubbish has been thrown. It is avoided by cattle (RUNGE 1980). *Urtica dioica* and *Rumex obtusifolius* occurring with presence class IV and III respectively are *Artemisietea* species too. Further differential species are *Poa supina (Plantaginetea)*, *Epilobium alpestre* and *Senecio nemorensis* (characteristic of the arctic-alpine tall herb communities of the *Betulo- Adenostyletea* Br. Bl. & Tx. 1943, and, with low presence class, *Impatiens noli-tangere*, *Chrysosplenium alternifolium* and *Ranunculus nemorosus* (*Alno-Padion*).

Columns 1–3 consist of relevés made by LIPPERT (1966) in the southeastern part of Germany (Berchtesgaden) at 600 m (relevés 1 and 2) and 860–1720 m (column 3). In columns 1 and 2 (one relevé each) *Plantaginetea* species are almost absent while *Molinio-Arrhenatheretea* species are preponderant and *Fagetalia* and *Artemisietea* species, though considerably less important, follow next (*table 2*). By the presence of *Oxalis acetosella (Fagion)*, the *Alno-Padion* species *Lysimachia nemorum*, *Stachys sylvatica*, *Brachypodium sylvaticum*, *Salvia glutinosa* (*Fagetalia*, also *Alno-Padion*), *Ranunculus nemorosus* (*Calthion*, also *Alno-Padion*) and the *Origanetalia vulgaris* Th. Müller 1961 species *Clinopodium vulgare*, *Origanum vulgare* and *Geranium sylvaticum* the forb fringe (scrub-grassland boundary zones) character of both relevés is indicated. The high coverage of *Rubus caesius* in relevé 1 expresses a very low grazing pressure. Lippert (1966) proposed to assign these *Mentha longifolia* communities to the *Chenopodietea*. As species of this class are absent this proposal is unfounded.

3.1.2. Conglomerate of Mentha longifolia and Epilobium palustre (column 4)

The conglomerate of *Mentha longifolia* and *Epilobium palustre* consists of 4 relevés made by CREDARO & PIROLA (1975) in Italy between 780 and 1650 m. According to these authors this *Mentha longifolia*- dominated vegetation has a

Table 1. Synoptic table of the mixtum compositum of *Mentha longifolia* conglomerates. In columns 1, 2, 13, 18–21 the cover-abundance values are indicated; in the other columns the presence class is given in Roman numerals (relevés more than 5) or in Arabic numerals (relevés less than 5). Besides the cover-abundance values have been presented when available. Locality: G = Germany, I = Italy, S = Spain, J = Yugoslavia, Cz = Czechoslovakia, R = Rumania. Syntaxonomic status: Ag = Agropyretea, Ar = Arrhenatheretalia, A.v. = Artemisietea vulgaris, B.A. = Betulo-Adenostyletea, Bi = Bidentetea, Ch. = Chenopodietea, Ep = Epilobietalia, Fa = Fagetalia, F.B. = Festuco-Brometea, FB/Ar = Festuco-Brometea/Arrhenatheretalia, G.S. = Glycerio-Sparganion, Ho = Holoschoenion, I.N. = Isoeto-Nanojuncetea, L.P. = Lolio-Potentillion, M.A. = Molinio-Arrhenatheretea, M.c. = Magnocaricion, M.C. = Montio-Cardaminetea, Mo = Molinietalia, Na = Nardetalia, Ph = Phragmitetea, Pl = Plantaginetea, Q.F. = Querco-Fagetea, SC = Scheuchzerio-Caricetea, T.G. = Trifolio-Geranietea. For additional infrequent taxa see appendix.

Tabel 1, (Continued)

	Column number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	Number of relevés	1	1	5	4	3	3	5	7	18	7	7	5	1	2	2	2
	Locality	G	G	G	I	G	G	S	G	G	GJS	R	J	J	S	S	G
SC	Carex nigra				1 +					II+-2							
	Differential species 10																
	Mentha rotundifolia										III+-4						
LP	Alopecurus geniculatus										II+-2						
	Differential species 11																
Ph	Mentha aquatica						1				I+	V+-2					1 +
Ph	Althaea officinalis										I+	V+-1	I2		2 2-3		
Bi	Polygonum lapathifolium										I+	V+-2	I+				
Mo	Lythrum salicaria						3			I+	I+	V+-1					
Ph	Lycopus europaeus									III+-1	II+	V+					
Ch	Xanthium strumarium											V+	III+-1				
Arm	Lotus tenuis											IV+					
Ph	Phragmites australis						1					IV+					
Mé	Scutellaria galericulata									I+		IV+					
GS	Veronica anagallis -aquatica											III+-1					
IE	Pulicaria vulgaris											III+					
Ph	Poa palustris											III+-2					
Bi	Chenopodium glaucum											III+-1					
Mo	Epilobium hirsutum									I+-2	I+	III+-1		+			
Ch	Echinochloa crus-galli										I+	III+					
Mo	Stachys palustris											III+	I+				
Mo	Senecio aquaticus										I+	III+-1					1 +
Mo	Carex vulpina						1				I+	III+					
Ph	Scirpus lacustris											II+					
	Rumex dentatus											II+					
Mo	Lycopus exaltatus											II+					
Mo	Carex melanostachya											II+					
	Differential species 12																
Pl	Lolium perenne				2 +-1		3	III+-2		I+	II+		V1-2				
	Pulicaria dysenterica								II		II+	III+	V1-3	+			2 1
Ch	Cichorium intybus									I+	I+		IV+-1				
LP	Rorippa sylvestris										I+		IV+				
Ch	Daucus carota					1			I	I+			III+-1				1 +
Ch	Galeopsis speciosa												III+-1				
Bi	Polygonum mite										I+		III+				2 2
Ch	Pastinaca sativa												II+				1 +
Pl	Cynodon dactylon												II1-2				
	Differential species 13																
Bi	Bidens tripartita									I+	I+	V+-1	V+-1	+		1 +	1 2
Av	Galega officinalis											III+	IV+-2				
LP	Mentha pulegium										I+	III+	III+	1			
Ch	Matricaria perforata	+										II+	II+				
Av	Artemisia vulgaris											II+	III+				
LP	Inula britannica											III+	III+				
	Differential species 14																
Ep	Carex divulsa													+			
Sp	Centaurium erythraea													+			
	Differential species 15																
	Kapeta nepetella														2 +-1		
Av	Dipsacus fullonum														1 1		
	Differential species 16																
Pb	Sanguisorba minor															1 +	
	Leontodon taraxacoides															1 +	
Ag	Convolvulus arvensis															1 1	
Ch	Setaria sp.															1	
	Differential species 17																
	Oenanthe banatica																
	Differential species 18																
Ch	Chenopodium album																
Ch	Diplotaxis tenuifolia																
MA	Vicia sepium																
Av	Calystegia sepium								I								
	Differential species 19																
MA	Arrhenatherum elatius																
Mo	Carex acutiformis																
Av	Crucista laevipes																
Mo	Phalaris arundinacea																
	Differential species 20																
Ch	Rumex pulcher																

Table 1, (Continued)

	Column number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
	Number of relevés	1	1	5	4	3	3	5	7	18	7	7	5	1	2	2	2	
	Locality	G	G	G	I	G	G	S	G	G	GJS	E	J	J	S	E	G	
	Remaining species																	
Ph	Galium palustre	+	1		4				III	II+-2	I1	IV+						2
	Ranunculus repens		1	V1-2		3	3		V	V1-3	V+-2	V+	IV+-1				2 +-3	3
Ag	Elymus repens			IV+-2		1		II+-1	I	I1	II+				2 +-1			
	Taraxacum officinale group			II1-1		2	3		II	III+	II+							
SC	Juncus articulatus				4 +-1	2	3	III+-1	I	IV+-2	II1				1 +			
GS	Veronica beccabunga				2 +					III+-2	I+						1 +	2
	Lysimachia nummularia						2		II	III+-2	II+-1	III+-1						3 +
	Festuca arundinacea				3 +-1			IV+-2	III						1 2			
Fe	Lysimachia nemorum	1	+	I1						I1								
	Trifolium hybridum					1	2				I1-3							1
	Agrostis capillaris					2	2		I									
	Calamagrostis varia	+	+	I+														
Fs	Stachys sylvatica	+	+	I1														
GS	Epilobium parviflorum							II1-3		IV+-1		III+						
Bi	Polygonum hydropiper									Ir	I+			+				
	Rumex conglomeratus									I1			III+-1					
FB	Euphorbia cyparissias	1	+	I+														
	Potentilla erecta	2	+		1 +					I+								
GS	Glyceria fluitans						1			I+	II+-3							
MC	Cardamine amara			I+	2 +-1													2
Ev	Galeopsis tetrahit								II	I+	I+							
Ho	Scirpus holoschoenus										I+				2 1-2			
	Torilis japonica																1	
	Torilis sp.							II+							2 +-1			
Na	Hypericum maculatum			I		1												
TG	Geranium sylvaticum		+	I1														
	Odontites verna								II		II+							
Na	Carex ovalis									I+								3 +
Fs	Stellaria nemorum			II1-2							I1							
SC	Carex echinata									I+-1								2
TG	Agrimonia eupatoria			I						II					1			
Ch	Picris hieracioides																	
	Bromus mollis L.																	

strong affinity to the *Molinietalia* which is confirmed by the data given in *table 2*. From the *Molinietalia* species *Equisetum palustre, Myosotis scorpioides, Juncus effusus* and *Geum rivale* have their highest frequency in the *Calthion*, tall meadows, often rich in tall forbs (KNAPP 1979). *Epilobium palustre* being differential for this conglomerate also occurs in the *Calthion* although it is typical of the *Caricion curto-nigrae*. CREDARO & PIROLA (1975) stress the unclear syntaxonomic position of this vegetation. They recorded it at water-saturated soils along brooks. It is inundated in spring and during periods with heavy rainfall. It has also been found in *Alnus incana*- and *Alnus viridis* woods. The influence of grazing is not mentioned by them.

The high coverage of *Deschampsia caespitosa* (2–3) probably indicates that grazing, if occurring at all, is only irregular, resulting in a selective advantage for this unpalatable grass species (KLAPP 1971). Under these conditions (selective low grazing pressure) more food is offered by the vegetation than needed, with the consequence that unpalatable species like *Deschampsia caespitosa, Festuca arundinacea* and *Urtica dioica,* are neglected by cattle (KLAPP 1965, DIRVEN & NEUTEBOOM 1975). When the stocking rate is high and herbage availability is low, the turf is kept uniformly short with no coarse vegetation (DUFFEY et al. 1974).

The systematic group value of the *Plantaginetea* including the *Lolio-Potentillion* as represented by *Lolium perenne, Agrostis stolonifera* and *Carex hirta*, is low.

3.1.3. Conglomerates of a) Mentha longifolia and Carex acuta and b) of Mentha longifolia and Alopecurus pratensis (columns 5 and 6)

These conglomerates have been described as respectively *Junco-Menthetum* variant of *Festuca rubra* (a) and variant of *Carex acuta* (b), by PFROGNER (1973). The first is the dry variant and is differentiated by *Molinio-Arrhenatheretea* and *Arrhenatheretalia* species; the latter, the moist variant, is differentiated by *Molinietalia* species.

Although *Mentha longifolia* has been recorded in only one of the relevés, both variants have been assigned to the *Junco-Menthetum* mainly because of the presence of *Juncus inflexus*. *Juncus inflexus* however occurs with high presence class in other communities, belonging to the *Lolio-Potentillion anserinae* (SÝKORA 1982 b and c). Like in the conglomerates discussed before, the group value of the *Molinio-Arrhenatheretea* is considerably higher than that of the *Plantaginetea*. The group values of the *Molinietalia* and *Arrhenatheretalia* confirm the differences between the variants as stated above *(table 2)*.

3.1.4. Conglomerate of a) Mentha longifolia and Deschampsia media (column 7) and b) Mentha longifolia and Scirpus holoschoenus (column 14)

These conglomerates have been described from Spain as *Junco-Menthetum longifoliae guadaricum* subassociation *typicum* (a) and subassociation of *Verbena-Althaea officinalis* (b) by RIVAS GODAY & CARBONELL (1961). The conglomerate

of *Mentha longifolia* and *Deschampsia media* is differentiated by *Trifolium pratense* and *Holcus lanatus (Molinio-Arrhenatheretea), Deschampsia media, Lotus uliginosus* and *Carum verticillatum (Molinietalia)* and by *Leontodon autumnalis (Arrhenatheretalia). Trifolium pratense* is susceptible to waterlogging and grazing by which it is negatively influenced; its presence therefore is a negative indication for the *Lolio-Potentillion.* Other differential species are *Ranunculus bulbosus, Briza media* and *Plantago media,* all occurring optimally in the *Mesobromion* but also in moderately dry *Arrhenatherion* communities. This group indicated in *table 1* by FB/Ar has a systematic group value of 22. The systematic group values of the *Molinio-Arrhenatheretea* and the *Plantaginetea* are almost equal, especially when the FB/Ar species are added. The total of the group value of *Molinio-Arrhenatheretea* and FB/Ar is 124. According to Rivas Goday & Carbonell *Mentha longifolia* is building facies with a nitrophilic tendency within the moist *Holoschoenetalia* and the *Molinietalia* of montane areas. Because of the anthropozoogenic and the nitrophilic character of the habitat they assign this community to the *Plantaginetea.* The authors describe the habitat of the conglomerate with *Scirpus holoschoenus (Junco-Menthetum* subassociation of *Verbena-Althaea officinalis)* as more nitrophilous and more ruderal which is indicated too by the presence of *Dipsacus fullonum, Verbena officinalis, Galium aparine, Eupatorium cannabinum* and *Nepeta nepetella,* all occurring preferentially in nitrophilous tall forb communities (*Artemisietea*). Although *Verbena officinalis* is considered a character species of the *Agropyro-Rumicion crispi* by Oberdorfer (1979), I assign this species to the *Artemisietea* because it is absent from wet soils and generally occurs in tall forb communities of the *Arction,* e.g. in the *Tanaceto-Artemisietum.* In contrast to the *Lolio-Potentillion* the *Arction* is intolerant of inundation. Within the conglomerate with *Scirpus holoschoenus* the *Molinio-Arrhenatheretea* and the *Artemisietea* have the highest group values. It is likely that the sites are hardly, if at all, grazed.

3.1.5. Conglomerate of Mentha longifolia and Senecio cordatus (column 8)

The relevés composing the conglomerate of *Mentha longifolia* and *Senecio cordatus* have been made in Germany by OBERDORFER (1957), between 120 and 900 m. Like the conglomerate of *Mentha longifolia* and *Rumex alpinus*, it has some affinity to the *Rumicetum alpini.* The differential species are *Senecio cordatus*, a character species of that association and *Cirsium arvense (Artemisietea).* The *Plantaginetea* have a systematic group value which is only slightly higher than that of the *Arrhenatheretea.* According to Oberdorfer the community forms a transiton to the *Artemisietalia* and the *Molinietalia.* It is a rather frequent community in wet depressions in meadows, along rivers, ditches or along roads under the influence of treading and grazing.

3.1.6. Conglomerate of Mentha longifolia and Hypericum tetrapterum (column 9)

In this conglomerate, based on relevés made in Czechoslovakia on altitudes of

350–800 m by BLAŽKOVÁ (1971), *Molinio-Arrhenatheretea* species are preponderant. *Plantaginetea* species are less important. *Table 1* shows that this column is differentiated very well, mainly by *Molinio-Arrhenatheretea* species. The *Molinietalia* are presented by *Hypericum tetrapterum* (*Filipendulion*, a tall forb community), *Mentha arvensis, Caltha palustris, Scirpus sylvaticus, Equisetum palustre* and *Myosotis scorpioides* (*Calthion*, meadows, often rich in tall forbs). *Glyceria plicata, Lycopus europaeus, Epilobium parviflorum, Veronica beccabunga* and *Carex paniculata* are representatives of reed communities from inundated sites. BLAŽKOVÁ noticed the considerable proportion of *Molinio-Arrhenatheretea* species in the *Junco-Menthetum* and she ascribed this to the close contact between these units. The *Junco-Menthetum* often is surrounded by *Molinio-Arrhenatheretea* (especially *Cynosurion*) communities. It forms very narrow zones, some metres to even only some decimetres wide zones between the pastures (meadows) and the source or brook and is only inundated for short periods. The community is absent in river valleys with prolonged inundations. Apart from the hydrology the saturation of the soil sorption complex with the cations Ca^{++} and Mg^{++} seems important.

The vegetation often consists of a mosaic of bunches of *Juncus inflexus* on which the *Arrhenatheretea* species grow and of depressions with *Phragmitetea*, particularly *Magnocaricion* species. Penetration of species from other communities is possible because of the open character of the vegetation; the soft, slimy soil surface is easily poached by cattle. According to BLAŽKOVÁ (1971), *Mentha longifolia* has a broader amplitude than *Juncus inflexus* and also penetrates into the fringes on the brook banks. On sites excluded from grazing the *Junco-Menthetum* occurs without any essential difference in floristic composition.

3.1.7. Conglomerate of Mentha longifolia and Mentha rotundifolia (column 10) and Junco-Menthetum rotundifoliae (columns 18, 23 and 24)

The communities presented under this section have been recorded by LOHMEYER (1953), OBERDORFER (1954 and 1957), TÜXEN & OBERDORFER (1958), LÜPNITZ (1967) and MARKOVIČ (1973) from Germany, Jugoslavia and Spain. A common feature is the presence of *Mentha rotundifolia*, a species of verges, roadside ditches, and walls bordering vineyards. It is more drought resistant and seems more thermophilous than the other species of the genus *Mentha* occurring in Europe. The species has a Westmediterranean-Atlantic distribution. The conglomerate of *Mentha longifolia* and *Mentha rotundifolia* (column 10) is a mixture of both species, in the other columns (18, 23, 24) the first species is lacking. The systematic group value of the *Plantaginetea* is considerably higher in the conglomerate, higher in column 24, almost equal in column 23 and lower in 18, than that of the *Molinio-Arrhenatheretea*. The *Mentha rotundifolia*-communities are differentiated against the conglomerate of *Mentha longifolia* by *Chenopodium album* and *Diplotaxis tenuifolia* (*Chenopodietea*), *Vicia sepium* (*Arrhenatheretalia*) and *Calystegia sepium* (*Convolvuletalia*). The *Artemisietea* and *Chenopodietea* element is pronounced. In column 24 in which *Mentha rotundifolia*

has its highest cover value (3–4), the systematic group value of the nitrophilic tall forb communities (*Artemisietea*) is equal to that of the *Plantaginetea*. This is in accordance with the statement of Runge (1980), that in recent times *Mentha rotundifolia* is spreading on ruderal sites.

The relevés made by OBERDORFER (1954) and LOHMEYER (1953) have been recorded on moderately grazed sites. According to MARKOVIČ (1973) the *Mentha longifolia* stands often are influenced by poaching and grazing. TÜXEN & OBERDORFER (1958) state that the community is sensitive to poaching and that when exposed to grazing it is easily disturbed during periods with high water levels. The lower distribution limit of *Mentha longifolia* is determined by the mean high water line in summer. *Mentha rotundifolia* occurs on relatively drier sites. the *Lolio-Potentillion* on the contrary has been observed to tolerate an even rather prolonged inundation during summer (SÝKORA, in prep.).

3.1.8. Conglomerate of Mentha longifolia and Mentha aquatica (column 11)

This conglomerate based on relevés made by POP (1968) from Rumania is differentiated by a large number of species viz. *Mentha aquatica, Althaea officinalis, Lycopus europaeus, Phragmites australis, Scutellaria galericulata, Veronica anagallis-aquatica, Poa palustris, Carex vulpina, Scirpus lacustris, Lycopus exaltatus* and *Carex melanostachya (Phragmitetea*, reed vegetation in more or less stagnant water), *Lythrum salicaria, Epilobium hirsutum, Stachys palustris* and *Lysimachia vulgaris* (*Filipendulion*, tall forb communities). Other differentials are *Polygonum lapathifolium, Chenopodium glaucum, Echinochloa crus-galli, Lotus tenuis* and *Pulicaria vulgaris*. The *Chenopodietea* species *Xanthium strumarium* and *Matricaria perforata* and the *Artemisietea* species *Galega officinalis* and *Artemisia vulgaris* are common differentials for this community and the conglomerate of *Mentha longifolia* and *Pulicaria dysenterica* (column 12, section 3.1.9). The preponderance of *Phragmitetea* species is clearly shown in *table 2*. According to Pop phytocoenoses of *Mentha longifolia* and *Juncus inflexus* form extensive and monotonous two layered stands from 100–200 m^2 to 500–1000 m^2 with a total height of 1 m.

3.1.9. Conglomerate of Mentha longifolia and Pulicaria dysenterica (column 12)

This conglomerate is based on relevés made by MARKOVIČ (1973) from the bank of a brook, from a road side ditch and from a pasture on the bank of the river Save (Jugoslavia). Although the *Plantaginetea* are preponderant there is a strong element of the *Chenopodietea* i.e. nitrophilous weed communities of rootcrop fields and waste places, with a preponderance of annuals. Apart from the species in common with the conglomerate with *Mentha aquatica*, the conglomerate with *Pulicaria dysenterica* is characterized by *Cichorium intybus, Daucus carota, Galeopsis speciosa, Pastinaca sativa (Chenopodietea), Lolium perenne, Cynodon dactylon (Plantaginetea), Polygonum mite (Bidentetea)* and *Pulicaria dysenterica*. According to OBERDORFER (1979) *Daucus carota* and *Pastinaca sativa* occur

preferentially in the *Dauco-Melilotion* and other *Onopordion* communities. In the western part of Europa these species are characteristic of the *Arrhenatheretum*.

Although *Pulicaria dysenterica* is considered to be a character species of the *Lolio-Potentillion anserinae* (previously named *Agropyro-Rumicion crispi* Nordh. 1940 em. Tx. 1950), it has only a negligible presence in the *Lolio-Potentillion* of the northern part of the Atlantic domain. Moreover, according to my own observations the species always occurs optimally in adjacent vegetation where grazing is prevented e.g. just beneath a fence, in tall reed vegetation out of reach of cattle, within patches of coarse vegetation (e.g. *Calamagrostis epigejos, Juncus effusus* or *Juncus maritimus*), or in ungrazed *Arrhenatheretea* stands ruderalized by irregular burning. The conglomerate of *Mentha longifolia* and *Pulicaria dysenterica* is influenced by cattle (MARKOVIČ 1973).

3.1.10. The remaining relevés (columns 13, 15–17, 19–22)

References: MARKOVIČ 1973, TÜXEN & OBERDORFER 1958, LANG 1973, HODISAN 1966, TODOR et al. 1971, OBERDORFER 1954.

In three of the remaining columns the *Plantaginetea* are preponderant (column 15 and 20) or are of equal importance compared to the *Molinio-Arrhenatheretea* (column 13). Column 15 was called the initial phase of the *Juncus inflexus-Mentha longifolia* association by TÜXEN & OBERDORFER (1958). In the other remaining relevés (except column 22) the *Molinio-Arrhenatheretea* have considerably higher systematic group values than the *Plantaginetea*. In column 22 which is dominated by the *Plantaginetea*, *Mentha longifolia* has a low cover value. As this relevé is recorded from a heavily poached and grazed site, this is quite understandable (OBERDORFER 1954). The relevé from column 19 is further characterized by *Artemisietea* and *Phragmitetea* species giving it the character of a tall forb-tall sedge community. This relevé was made by LANG (1973) on the bank of a brook in the vicinity of a farm. The site was grazed by geese.

3.2. Concluding remarks concerning the mixtum compositum with Mentha longifolia and Mentha rotundifolia.

Mentha longifolia occurs more often in conglomerates in which *Molinio-Arrhenatheretea* species are preponderant than in conglomerates dominated by *Plantaginetea* species (*table 4*). In the conglomerate of *Mentha longifolia* and *Mentha aquatica* the *Phragmitetea* constitute the main element. Since there is no objective criterion to assign the conglomerates to one of these classes and since the floristic composition of the various conglomerates differs considerably, I consider the association *Junco-Menthetum longifoliae* as non-existing. To quote BRAUN-BLANQUET (1928): (translation by me) "The potential number of species combinations is unlimited. Typification of every combination realised in nature would lead to a chaotic shivering of the vegetation units." The conglomerates are mosaics of mainly *Molinio-Arrhenatheretea* and *Plantaginetea* fragments with, in several cases, *Artemisietea, Phragmitetea* or *Chenopodietea* added. According to Blažková (personal communication 1982) these mosaics are com-

Table 4. Summary of the importance of *Molinio-Arrhenatheretea, Plantaginetea* and *Phragmitetea* species in I) the conglomerates with *Mentha longifolia* and II) in the *Junco-Menthetum rotundifoliae.*

I	*Molinio-Arrhenatheretea* species distinctly preponderant in 11 clusters (26 relevés)
	Molinio-Arrhenatheretea species preponderant in 1 cluster (18 relevés)
	Total: 12 clusters (44 relevés).
	Plantaginetea species distinctly preponderant in 5 clusters (16 relevés)
	Plantaginetea species slightly preponderant in 2 clusters (12 relevés)
	Total: 7 clusters (28 relevés)
	Plantaginetea and *Molinio-Arrhenatheretea* species of equal importance in one relevé
	Phragmitetea species distinctly preponderant in 1 cluster (7 relevés)
II	*Plantaginetea* species of equal importance as the *Artemisietea* species but preponderant over the *Molinio-Arrhenatheretea* species in 1 cluster (4 relevés).
	Plantaginetea species of equal importance as the *Molinio-Arrhenatheretea* species in 2 clusters (7 relevés)

posed of mixtures of wet, frequently inundated microsites alternating with moist, relatively drier ones, caused partially by the influence of grazing and partially by the tussocks formed by species like *Juncus inflexus, Festuca pratensis* and *Deschampsia caespitosa.* Under extensive grazing conditions the *Plantaginetea* are of minor importance only. Intensification of grazing favours the *Plantaginetea* element but at the same time the coverage of *Mentha longifolia* decreases. Most of the conglomerates especially those with a preponderance of *Molinio-Arrhenatheretea* species have a tall forb structure, thus reflecting the low grazing pressure. Patches of ungrazed tall herbs e.g. *Mentha longifolia, Festuca pratensis* and *Deschampsia caespitosa* alternate with patches poached by cattle. Usually the *Mentha* species remain ungrazed. This is what Runge (1980) pointed at when he remarked that the *Junco-Menthetum* is avoided by cattle. Also, Blažková (personal communication 1982) reported the *Junco-Menthetum* from several ungrazed sites and stated that the development of this community is not strictly bound to the grazing factor. That the *Lolio-Potentillion* is restricted to grazed, regularly inundated pastures, is in accordance with the phytosociological conclusion by which *Mentha longifolia* can not be considered a representative of this alliance. The tall forb habitus of *Mentha longifolia* and the tall forb structure of the *Junco-Menthetum* have also been remarked by HEGI (1975) and TÜXEN (1956). According to Hegi *Mentha longifolia* is especially growing abundantly in montane and subalpine tall forb communities. The *Juncus inflexus-Mentha* longifolia association has been described by TÜXEN (1956) as a tall forb community rich in hemicryptophyta reptantia. It may be concluded that the epharmony of this species is comparable to that of the *Filipendulion* species. According to NEUHÄUSL & NEUHÄUSLOVA-NOVOTNA (1975) the *Filipendulion* communities are rather heterotoneous. Poaching causes the infiltration of nitrophilous *Agropyro-Rumicion* Nordh. 1940 em. Tx. 1950 species (see SÝKORA 1980).

The floristic composition of the *Junco-Menthetum rotundifoliae* is very similar to that of the conglomerate of *Mentha longifolia* and *Mentha rotundifolia.* As

such it is floristically heterogenous and not sufficiently characterized by a species combination of its own. Furthermore insufficient relevés of this community are available. This leads me to the conclusion that the establishment of this community as an association at present must be rejected.

4. CARICETUM VULPINAE Tüxen 1947

(For enumeration of papers dealing with this association we refer to the appendix.)

The *Caricetum vulpinae* is characterized by the character species *Carex vulpina* and by the presence of a considerable number of *Magnocaricion* species and other species of the *Phragmitetea* (see *table 5*). This justifies its assignment to the above mentioned syntaxa. Due to the absence of grazing the systematic group value of the *Plantaginetea* is considerably lower (*table 3*). As their hydrologic requirements are similar the *Caricetum vulpinae* is replaced by the *Lolio-Potentillion* under the influence of grazing (GÉHU 1961). In this respect it is significant that even a *carex vulpina* variant of the *Rumici-Alopecuretum geniculati* has been described (FREITAG 1957, GÉHU 1961, MEISEL 1977).

After the construction of the synoptic table a division into subassociations appeared to be impossible. The subassociations described in the literature have only a local significance. Tabulation according to the sequence along the first axis of a principal components analysis shows the gradual increase along this axis of the *Molinio-Arrhenatheretea*, especially the *Molinietalia* as well as that of the *Scheuchzerio-Caricetea* (*table 5* and *fig. 3*). This change in floristic composition reflects a decrease in the amplitude of fluctuations in the water table. The occurrence of the *Molinietalia* indicates a situation in which both the inundation and the desiccation are less severe (BALATOVA-TULÁČKOVÁ 1968). The hydrology of the *Caricetum vulpinae* stands at the left side of the ordination diagram corresponds with that of the *Ranunculo-Alopecuretum geniculati*, while that of stands at the right side is more characteristic of the *Triglochino-Agrostietum stoloniferae* (SÝKORA 1982a, b and c).

As *Carex vulpina* is a poikilohygrophyte (BOUCHAT 1981) the *Caricetum vulpinae* is able to colonize sites where hydrophase, limose ecophase and terrestrial ecophase (HÉJNY 1960) are alternating e.g. on river banks, along ponds, in former river beds and in depressions without discharge, mainly on mineral gley soils rich in silt. Mineralization is enhanced by the fluctuating water table. The association has a northern continental distribution with its highest occurrence in the eastern part of central Europa (WESTHOFF & DEN HELD 1969, OBERDORFER 1977).

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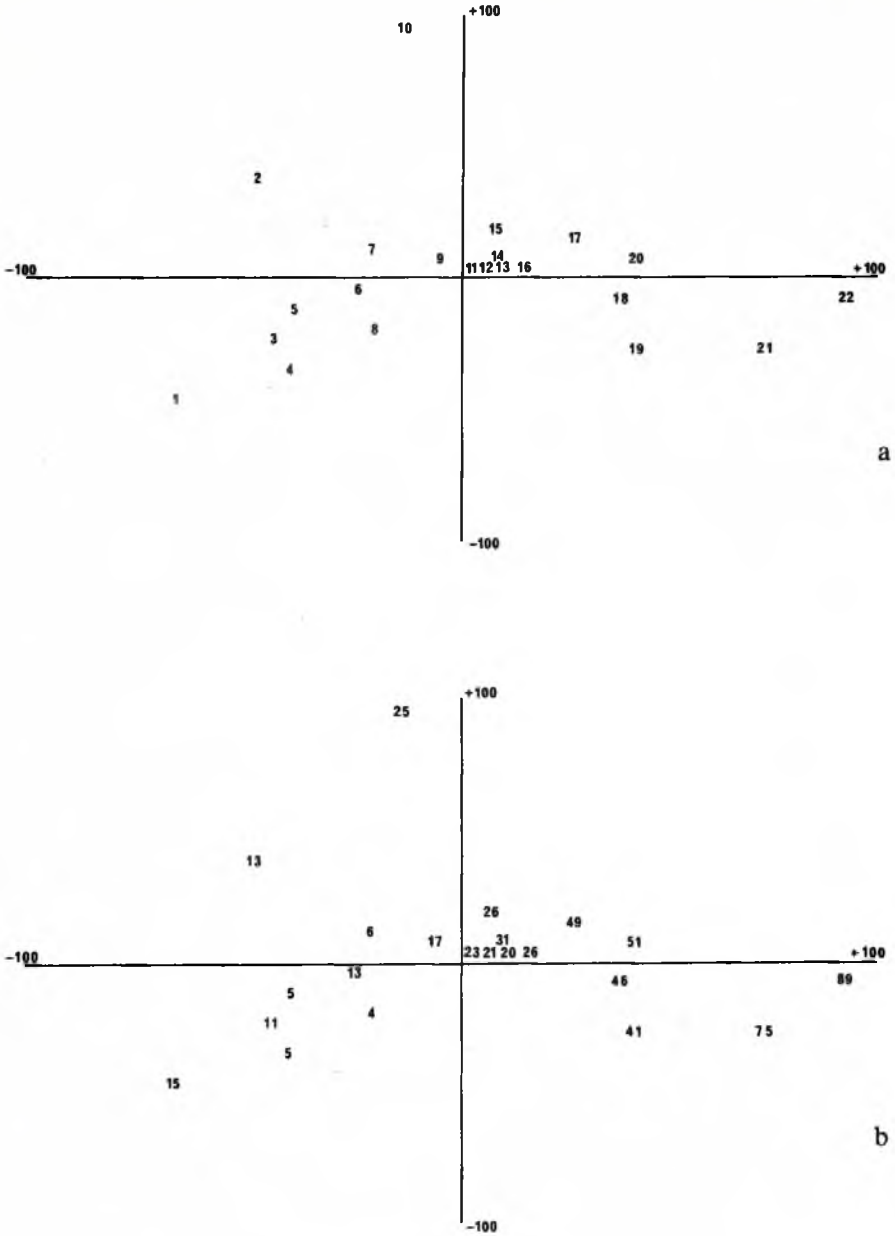
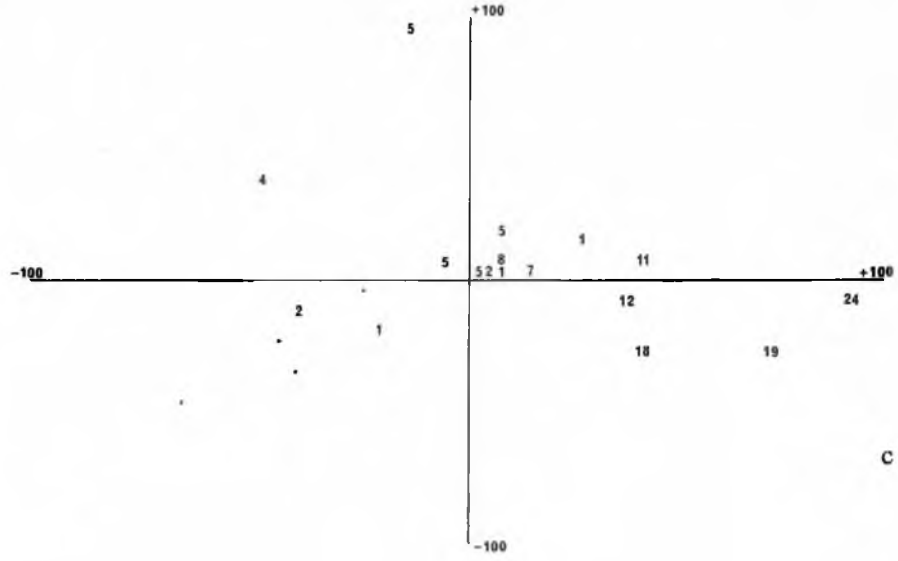


Fig. 3. Principal components analysis of the *Caricetum vulpinae*. Indicated are : (a) the column numbers (corresponding with the numbers in *table 5*); (b) the sum of the presence class values of the *Molinio-Arrhenatheretea*; (c) the sum of the presence class values of the *Scheuchzerio-Caricetea*, and (d) the sum of the presence class values of both the *Molinio-Arrhenatheretea* and the *Scheuchzerio-Caricetea*.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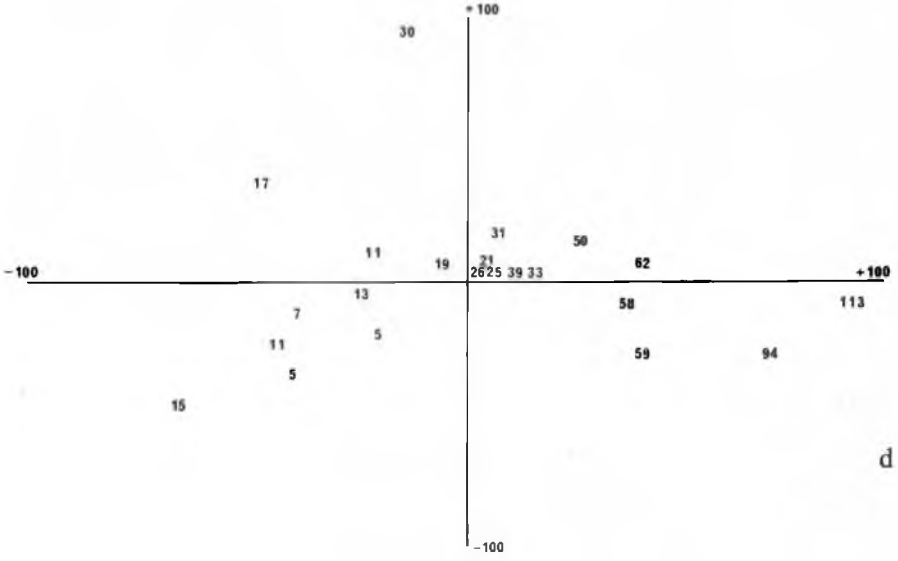
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APPENDIX

Additional species of the mixtum compositum of *Mentha longifolia*

Table 1.

Column nr. 3: Tozzia alpina (+), Thelypteris limbosperma (+), Rhinanthus aristatus (+), Phleum hirsutum (+), Petasites albus (+), Myosotis sylvatica (+), Mycelis muralis (+), Silene dioica (1), Equisetum sylvaticum (1), Aconitum napellus (r, 2);

Column nr. 5: Trifolium dubium (1);

Column nr. 6: Carex panicea (1), Scorzonera humilis (1), Symphytum officinale (1), Alisma plantago-aquatica (1), Polygonum amphibium (1);

Column nr. 8: Polygonum amphibium (I), Lamium album (I), Tanacetum vulgare (I) Carduus crispus (I), Geranium pratense (I), Senecio jacobaea (I), Senecio erucifolius (I);

Column nr. 9: Carex panicea (I), Carex otrubae (I), Vicia cracca (I), Valeriana dioica (I), Trifolium medium (I), Trifolium dubium (I), Sagina procumbens (I), Philonotis fontana (I), Galium verum (I), Epilobium roseum (I), Eleocharis mamillata (I), Cratoneuron filicinum (I), Ajuga reptans (I), Trisetum flavescens (+), Triglochin palustris (+), Stellaria media (1), Scrophularia umbrosa (1), Salix purpurea (+), Rhytidiadelphus triquetrus (+), Ranunculus flammula (1), Primula elatior (+), Polygonum amphibium (+), Platyhypnidium riparioides (2), Pedicularis palustris (+), Dactylorhiza majalis (+), Linum catharticum (+), Juncus bufonius (+), Hygrohypnum luridum (1), Geranium palustre (1), Euphorbia palustris (+), Eleocharis quinqueflora (+), Cirsium canum (1), Carex tomentosa (+), Carex remota (+), Cardamine pratensis (+), Campylium stellatum (1), Anagallis arvensis (+), Aegopodium podagraria (+);

Column nr. 10: Setaria pumila (+), Sambucus ebulus (+), Salix purpurea (+), Salix amplexicaulis (+), Populus nigra (1), Petasites hybridus (+), Oenanthe crocata (+), Melilotus altissima (2), Gratiola officinalis (+), Festuca gigantea (1), Eleocharis palustris (+) Cyperus sp. (+), Crepis capillaris (+), Centaurium erythraea (+), Barbarea sp. (+), Alliaria petiolata (+), Aegopodium podagraria (+);

Column nr. 12: Atriplex patula (+), Myosoton aquaticum (+), Malva sylvestris (+);

With presence class I or II in column nr. 23: Galium mollugo, Bromus sterilis, Capsella bursa-pastoris, Geranium molle, Sagina procumbens, Veronica arvensis, Veronica serpyllifolia, Rumex acetosa, Carex ovalis, Stellaria graminea, Agrostis capillaris, Linaria vulgaris, Hypericum tetrapterum, Epilobium roseum, Holcus lanatus, Festuca rubra, Symphytum officinale, Lysimachia nummularia, Glechoma hederacea;

With presence 1 or 2 in column nr. 24: Cynodon dactylon, Festuca pratensis, Carex vulpina, Raphanus raphanistrum, Ranunculus acris, Trifolium pratense, Pastinaca sativa, Lythrum salicaria, Hypochoeris radicata, Crepis capillaris, Picris echioides, Sonchus asper.

Additional species of the *Caricetum vulpinae*

Table 5.

Column nr. 2: Rumex conglomeratus (1), Mentha longifolia (1), Groenlandia densa (1);

Column nr. 4: Stachys palustris (I), Urtica dioica (I);

Column nr. 5: Althaea officinalis (I);

Column nr. 6: Lycopus europaeus (I), Juncus gerardi (I), Lotus tenuis (I), Myosurus minimus (I), Acorus calamus (I), Sagittaria sagittifolia (I);

Column nr. 8: Carex riparia (I), Rumex hydrolapathum (I), Eriophorum angustifolium (I), Rorippa lippizensis (I);

Column nr. 9: Carex elata (I), Peucedanum palustre (I), Scutellaria galericulata (I), Carex rostrata (I), Juncus filiformis (I), Silaum silaus (I);

Column nr. 12: Acorus calamus (+);

Column nr. 13: Ajuga reptans (I);

Column nr. 14: Eriophorum angustifolium (+), Trifolium pratense (1), Trifolium medium (+), Trifolium campestre (+), Thalictrum lucidum (+), Teucrium scorodonia (+), Stellaria graminea (+), Scirpus sylvaticus (1), Rumex hydrolapathum (+), Rumex aquaticus (+), Rhinanthus rumelicus (+), Potentilla erecta (+), Polygonum persicaria (+), Polygonum bistorta (1), Pedicularis palustris (1), Nardus stricta (+), Lythrum virgatum (+), Lotus corniculatus (I), Juncus gerardi (+), Juncus conglomeratus (+), Juncus compressus (I), Glechoma hederacea (+), Cirsium rivulare (+), Cichorium intybus (+), Carex rostrata (+), Carex riparia (+), Carex otrubae (I), Carex lepidocarpa (+), Carex flava (I), Carex elata (I), Calliergon giganteum (+), Calamagrostis epigejos (+), Bromus commutatus (+), Althaea officinalis (+), Achillea millefolium (+);

Column nr. 15: Scutellaria galericulata (I), Brachythecium rutabulum (I), Juncus filiformis (I);

Column nr. 16: Juncus filiformis (I), Phleum pratense (I);

Column nr. 17: Scirpus sylvaticus (+), Rumex hydrolapathum (+), Rumex aquaticus (r), Carex paniculata (+);

Column nr. 18: Selinum carvifolia (+), Rhytidiadelphus squarrosus (+);

Column nr. 19: Scutellaria galericulata (I), Equisetum arvense (1);

Column nr. 20: Scirpus sylvaticus (I), Rhinanthus minor (I), Mnium sp. (+), Geum rivale (+), Festuca rubra (+), Cerastium fontanum (+);

Column nr. 21: Serratula tinctoria (+), Scirpus sylvaticus (+), Rhinanthus minor (+), Ranunculus sceleratus (r), Polygonum hydropiper (1), Polygonum commutatum (+), Luzula multiflora (+), Festuca rubra (+) Festuca pratensis (I), Cynosurus cristatus (+), Carex curta (+), Carex brizoides (+), Bromus racemosus (+), Brachythecium rivulare (I), Ajuga reptans (+), Agrostis capillaris (+);

Column nr. 22: Allium angulosum (I), Centaurium erythraea (+), Eriophorum angustifolium (+), Linum catharticum (+), Parnassia palustris (I) Selinum carvifolia (+), Senecio jacobaea (+), Viola palustris (+) Valeriana officinalis (+), Trifolium campestre (I), Thalictrum angustifolium (I), Scutellaria galericulata (I), Scirpus sylvaticus (+), Potentilla erecta (I), Myosoton aquaticum (+), Cerastium fontanum (I), Cerastium arvense (+), Centaurea jacea (+), Carex elongata (+), Carex curta (+), Bellis perennis (+).

Author quotation for the *Caricetum vulpinae*

Balatova-Tulačkova 1965 (column nr. 20), ibid. 1968 (c. 17), ibid. 1976 (c. 14 & 17); Blažkova 1973 (c. 18 & 21); Bournerias et al. 1976 (c. 1,3 & 7), Van Donselaar & Van Leeuwen 1957 (c. 17); Falinski 1966 (c. 14); Géhu 1961 (c. 17, 18 & 20); Grigore 1971 (c. 6); Grigore & Coste 1976 (c. 14); Kovar, 1981 (c. 17); Meisel 1977 (c. 4, 15, 16 & 19), Mititelu & Barabas 1975 (c. 5); Oberdorfer 1957 (c. 13), ibid. 1977 (c. 9); Passarge 1964 (c. 8 & 11); Ratiu 1971 (c. 14); Rivas Goday & Carbonell 1961 (c. 2); Spanikova 1971 (c. 14 & 20); Van der Steeg (pers. comm.) (c. 10); Tüxen 1954 (c. 12); Walther 1977 (c. 12, 14, 18); Wilzek 1935 (c. 22).

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PUBLICATION VI

A SYNECOLOGICAL STUDY OF THE LOLIO-POTENTILLION ANSERINAE TÜXEN 1947 BY MEANS OF PERMANENT TRANSECTS. I: BRACKISH STENOSALEUTIC HABITATS.

Karel Vaclav Sýkora , Botanisch Laboratorium, Afdeling Geobotanie, Katholieke Universiteit, Nijmegen.

Change is the most important attribute of any plant community.

R.W.Becking 1968

Summary

In order to study the long term dynamics in the *Lolio-Potentillion*, four transects, located in the province of Zeeland, were studied during three consecutive years, from 1979 to 1981. The zonal differentiation of the plant cover has been determined by single linkage clustering and the floristic composition and syntaxonomic status of every zone has been described. A correlation was found between the zonation and the spatial pattern of the hydrological dynamics. The *Lolio-Potentillion* occurs optimally on places flooded in winter and spring. On soils which are waterlogged during the greater part of the year, the species characterizing this alliance also occur on non-flooded sites. Climatic oscillation resulted in an ecotopic fluctuation of many species. Species characteristic of the *Lolio-Potentillion*, the *Phragmitetea* and the *Bidention* were stimulated by the extra inundation in the summer of 1980. In the same year in the upper non-flooded zone *Molinio-Arrhenatheretea* species were stimulated by the high precipitation in July.

1. Introduction

From 1978 to the end of 1981 I studied the *Lolio-Potentillion anserinae* Tüxen 1947 in the Netherlands, Ireland, Belgium, N.-W. France, South-Sweden, England and Wales. The results of this research have been published in previous papers (SÝKORA 1980, 1982 a,b and c). As the sample plots were visited only once and as the *Lolio-Potentillion* occurs in a very dynamic environment, in these papers the main emphasis was necessarily laid on syntaxonomy. In 1980 I separated this alliance from the *Agropyro-Rumicion crispi* NORDH. 1940 em.TÜXEN 1950, since the floristic assemblage as well as the habitat of the former are largely at variance with the latter.

The *Lolio-Potentillion* is restricted to pastures occurring on soils which vary in nutrient availability from rich to moderately poor and which are inundated in winter and spring. In order to study the long term dynamics, permanent transects were laid in riverine habitats (1978) and in brackish habitats (1979). Apart from the difference in salt content of the soil, these habitats differ in hydrological dynamics. The brackish habitats discussed in this paper belong to the stenosaleutic ecotope, i.e. the difference between maximum and minimum water level does not exceed 60 cm. The riverine habitats (SÝKORA in prep.) on the contrary are eurysaleutic, i.e. the difference between maximum and minimum water level is considerably exceeding 80-100 cm and in most cases even surpasses five meters. For further explanation of the concepts used above I refer to KOPĚCKY (1969).

During the present research the main attention has been paid to the duration and the frequency of inundation. The hydrology is the master factor for the occurrence and the inner differentiation of the *Lolio-Potentillion* (SÝKORA 1982 a, b and c). In many cases hydrological conditions chiefly determine the zonal differentiation of the plant cover, the species composition and the production of biomass in the vegetation units (ADRIANI 1945, MÜLLER 1956, HEJNÝ 1960, STOFFERS & KNAPP 1962, NIEMANN 1963, 1970, HUNDT 1964, BALÁTOVÁ-TULÁČKOVÁ 1968, WALTHER 1977, ROZEMA 1978, BOEDELTJE & BAKKER 1980, GROOTJANS 1980, THOMAS et al. 1981 and others).

The aim of the present paper is to describe 1) a) the presence and

nature of boundaries and b) the zonal differentiation of the plant cover in relation to duration of submersion and 2) the effects of yearly fluctuations in rainfall and of duration and frequency of flooding on the contributions of the species to the sward.

According to TÜXEN (1950, 1957) these fluctuations may lead to considerable changes in the quantitative occurrence of the species from year to year. For this phenomenon TÜXEN introduced the term "Pendel-Sukzession" (shuttle succession) or "Harmonika-Sukzession" (concertina succession; translation by present author). Often during a shuttle succession even associations can alternate. VAN LEEUWEN extended the concept to include the alternating contraction and expansion of vegetation patches (1958). To my opinion it is recommendable to distinguish between changes by which an association develops into another one (succession) and minor reversible changes (fluctuations). If associations alternate the concept shuttle succession is synonym to cyclic succession (KNAPP 1974, MILES 1979). The term "ecotopic fluctuations" (RABOTNOV 1974) i.e. fluctuations caused by changes in the ecotope (climate, soil, hydrology) is applicable to the changes described in this paper.

2.Methods

2.1. Physical set up of the transects

In 1979 in the province of Zeeland four transects were made on slopes perpendicular to the waterline. Three of the transects are situated on the banks of former creeks, now surrounded by polders (Vlaamse Kreek, Cambron and Koegat) and one transect occurs on the bank of a clay pit adjacent to the inland slope of a sea dike (Inlaag Anna Friso). Their length is respectively 10, 26.5, 36.5 and 10 meters. Each transect was chosen in that way that it contained a stand of a *Lolio-Potentillion* community as well as two adjacent communities so that the transect constituted a sequence. In the case of Cambron however, the adjacent community at the lower end of the slope was missing.

The variation in length of the transects depends on the inclination of the slope. On steeper slopes the zonation is telescoped.

2.2. Analytical research phase

The transects were sampled by means of contiguous quadrats sized 0.5 x 2 meters at right angles to the transect line. For estimation of the quantitative occurrence of each species the Braun-Blanquet scale as refined by BARKMAN et al. (1964) was used (WESTHOFF & VAN DER MAAREL 1973).

In all sites the free water table was recorded by local gauges to which the soil surface of the transects was levelled (fig.3 a-d). The soil water table was also measured by means of three pipes along each transect (fig.2). Monthly totals of precipitation and evaporation recorded at Flushing are given in fig.11. From four sampling sites at each transect soil samples (depth 1-6 cm) were collected at intervals of three to four weeks. They were analysed in the laboratory for Cl^-, NH_4^+, NO_2^- and NO_3^- .Apart from these, organic content, soil texture, pH, total available N and P, PO_4^{3-}, $CaCO_3$ and pore volumes were determined only once. The pore volumes of 100 cc soil samples (depth 1-6 cm) were measured by means of a vacuum air pycnometer according to LANGER. For the other parameters samples were collected from clearly visible soil layers at any depth.

The data on the salinity of the surface water (Anna Friso) have been obtained from the Department for the Maintenance of Dikes, Roads, Bridges and the Navigability of Canals (Rijkswaterstaat).

2.3. Synthetical phase

The species were positioned in the tables (tables 1-4) in a way clearly showing their distribution along the transects. By means of single linkage clustering using the similarity ratio (WISHART 1969, 1975) dendrograms were constructed for the detection of boundaries (fig.6-9). The threshold values indicated in the dendrograms were set on similarity levels resulting in main clusters which are clearly definable by means of differential species.

The extended scale of BARKMAN et al. (1964) was transformed into a 1-9 numerical scale according to the ordinal transformation (VAN DER MAAREL 1979). With the help of these dendrograms and the data on the periods of flooding (fig.1) the tables have been divided into an upper,

a middle and a lower part (Vlaamse Kreek, Anna Friso), or into an upper and a lower part (Cambron and Koegat).

The sum of the transformed cover-abundance values of every species in each part of the table was compared from year to year in order to calculate the decrease or increase of the species (table 5).

Species nomenclature follows the Flora Europaea (TUTIN et al. 1964-1980) for phanerogams and LANDWEHR (1966) for bryophytes.

3. Results

3.1.The transects

3.1.1. Abiotic environment

Hydrology (fig.1 a-d and fig.2 a-d): lowest ground water levels measured in the upper part of the transects are respectively -117 cm (Cambron), -90 cm (Vlaamse Kreek), -49 cm (Anna Friso) and -47 cm (Koegat). The highest ground water level was situated at or very near to the soil surface. Lowest ground water levels measured in the lower part of the transects are respectively about -15 cm (Cambron,Vlaamse Kreek and Koegat) and -24 cm (Anna Friso). Highest water level: + 28 cm (Vlaamse Kreek), +23 cm (Cambron), +21 cm (Anna Friso) and +18 cm (Koegat). For the location of the pipes see fig. 3 a-d.

Salinity (fig. 4 and 5): the terminology of salinity degrees has been used according the Venice System (BEEFTINK 1962, 1965, RANWELL 1972). The Cl^- -content of the soil fluctuates throughout the year. The lower quadrats of the transects Anna Friso and Koegat have the highest salinity. While the ground water of the Koegat is oligohaline all the time, it reached a *B*-mesohaline value in August 1980 in the transect Anna Friso. On that moment sea water was probably percolating underneath the dike. In the upper quadrats the ground water level was higher than the free water level in the clay-pit (fig.3a) and on the date of sampling water has actually been seen to well up from the hole made by the auger. The chloride content of the free water corresponds with these data; it belongs to the oligohalinicum most of the time, but *B*-mesohaline values are reached during shorter periods (fig.5). The ground water in the

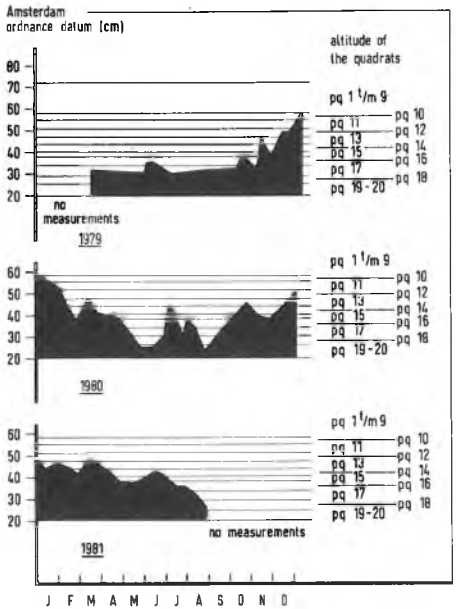


fig.1a Periods and depths of flooding in the transect Anna Friso.

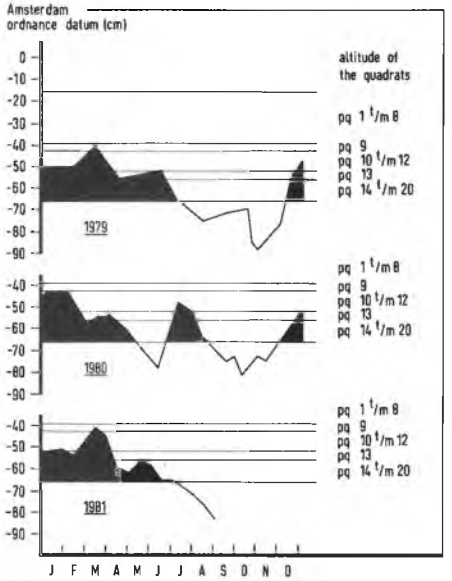


fig.1b Periods and depths of flooding in the transect Vlaamse Kreek.

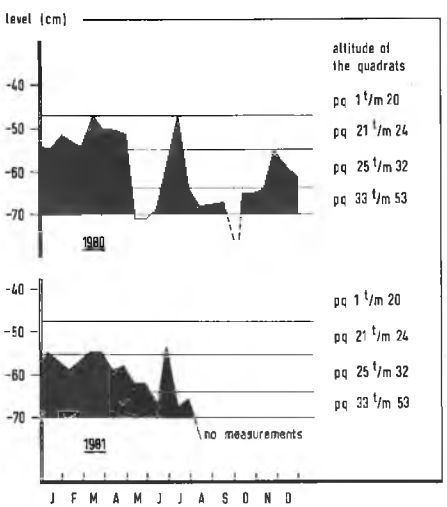


fig.1c Periods and depths of flooding in the transect Cambron.

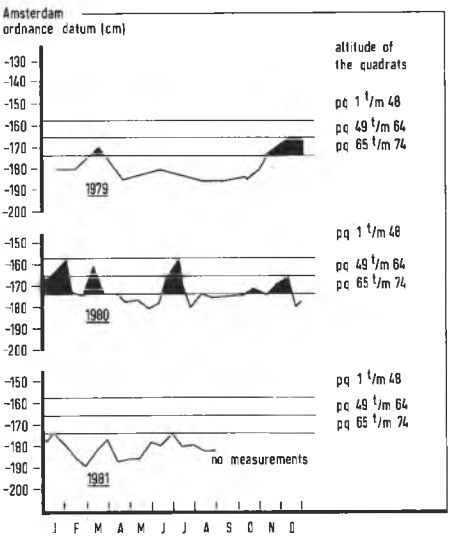


fig.1d Periods and depths of flooding in the transect Koegat.

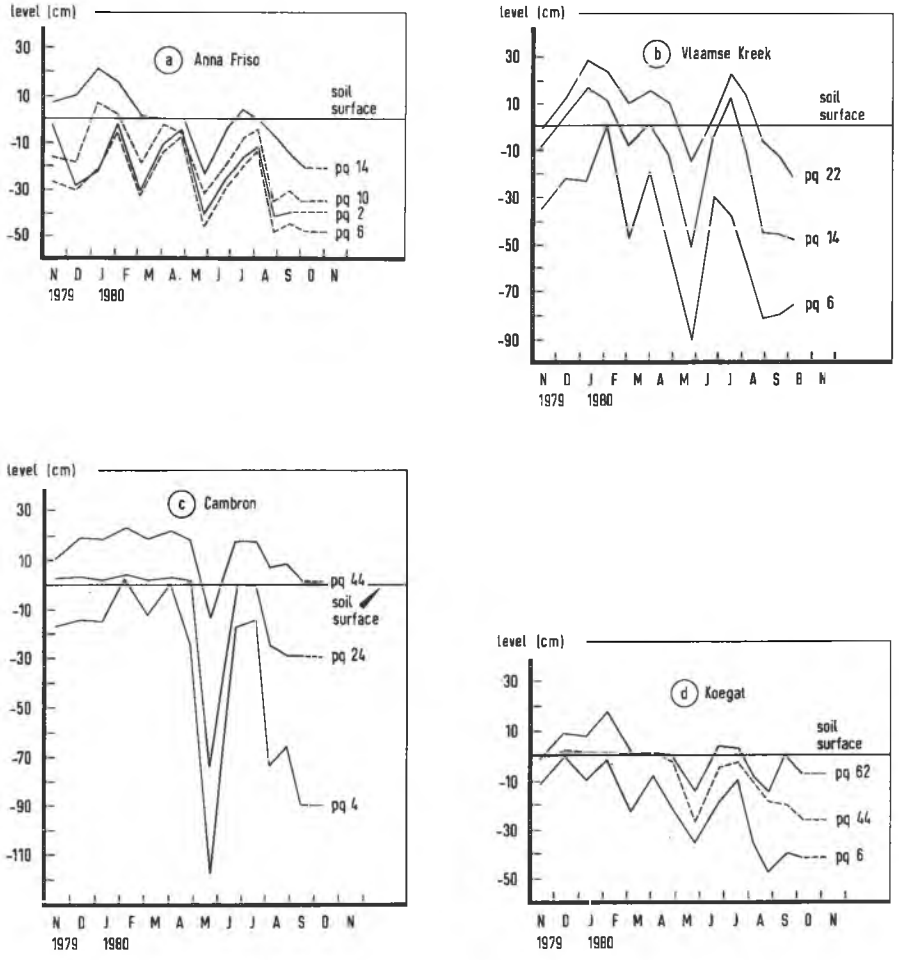


fig.2 The variation in the ground water level (duration curves) in a) Anna Friso; b) Vlaamse Kreek; c) Cambron; d) Koegat.

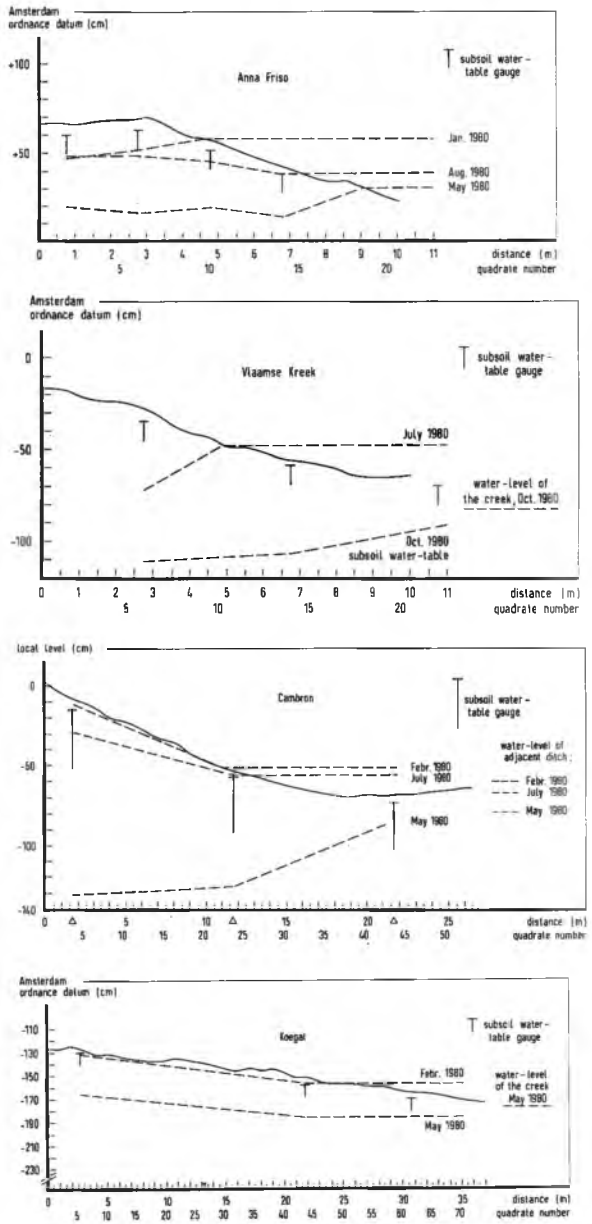


fig.3 Profile of the belt transects (uninterrupted line).a) Anna Friso; b) Vlaamse Kreek; c) Cambron; d) Koegat. The interrupted lines indicate the position of the (ground)water level on the given data. In figs.b & d the free water level of the creek and in fig.c that of a ditch adjacent to the transects are indicated in the right side of the figure.

lower part of the transect Vlaamse Kreek is alternately oligohaline or fresh. In the transect Cambron the oligohalinicum is only reached occasionally. The higher quadrats of all transects contain fresh ground water.

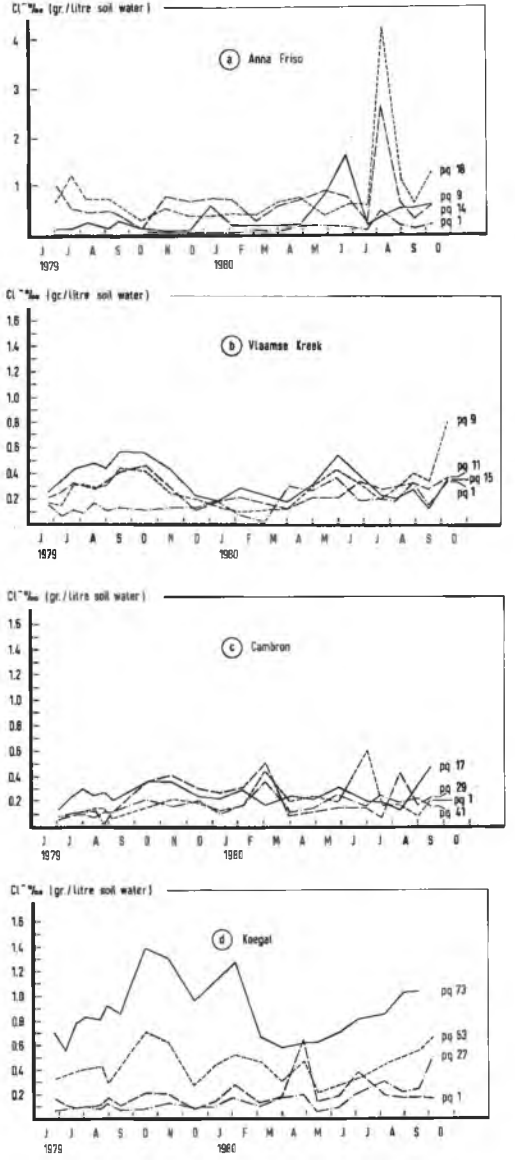


fig.4 The chloride concentration of the soil water in four quadrats of the transects. a) Anna Friso;b) Vlaamse Kreek;c) Cambron;d) Koegat.

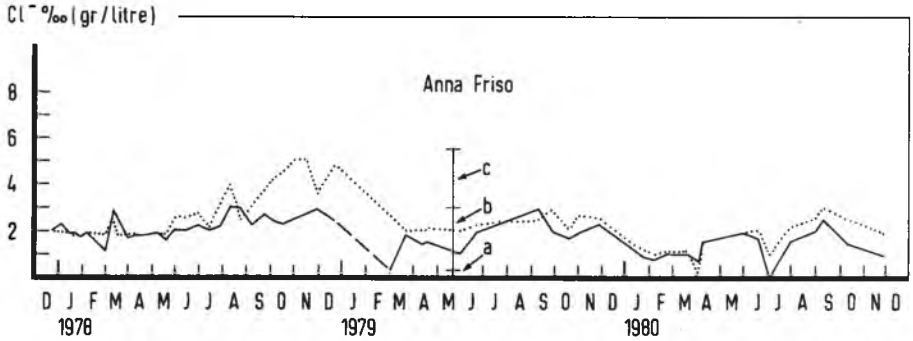


fig.5 The chloride concentration of the free water table of the Anna Friso on two different sampling points near the transect. (a= fresh water, b= oligohaline, c= *B*-mesohaline).

Soil texture and organic material content (MILLAR et al. 1958).

Transect Anna Friso: top soil: sand mixed with 23-33 % organic material.
subsoil : sand, organic material 1-2 %.

Transect Vlaamse Kreek: top soil: loamy sand to sandy loam, organic material 20-32 %.
subsoil: sand, organic material 4-5 %.

Transect Koegat: top soil: loam to clay loam, lower part of the transect sandy loam, organic material upper half of the transect 20-24 %, lower half 10-17 %.
peat layer on a depth of 35-70 cm; organic content 82 and 89 % (quadrats 1 and 13) and 49 % (quadrat 71).

Transect Cambron: top soil: sandy loam to sandy clay loam, lower part of the transect clay loam; organic material 21-26 %.
subsoil: sandy loam, lower part of the transect clay loam, organic content 4 (upper part) -13 % (lower part of the transect).

Pore volumes

The pore volumes reach high values in each transect: Koegat 76-82 %, Cambron 66-78 %, Anna Friso 66-71 % and Vlaamse Kreek 57, 60 and

75 % (p.q. 1, 9 and 13 respectively). For comparison we mention data given by BOEKER (1957): *Mesobrometum* 63 % and 59 %, *Seslerio-Xerobrometum* 65 %, *Xerobrometum* 61 %, *Schoenetum ferruginei* 79 %, *Lolio-Cynosuretum* 45 %, *Nardetum strictae* 71 %. The air filled pore volumes are however low: Koegat 5-10 %, Cambron 3-8 %, Anna-Friso 6-14 % and Vlaamse Kreek 4-8 % (date of sampling 25/6 and 2/7, besides in transect Cambron 20/9).

Calcium carbonate

In all transects the calcium carbonate values increase from the upper part to the lower. Values for the transect Anna Friso are very low, in all cases below 2 %. The calcium carbonate content of the other transects is high; Vlaamse Kreek 8-20 %, Cambron 12-31 %, Koegat 24-61 %. Shells were often present in the soil samples.

Although the calcium carbonate values for the transect Anna Friso are considerably lower compared to those for the other transects, this difference is not expressed in the floristic composition. While calcifuge species are absent, species commonly occurring in calcareous grasslands (e.g. *Carex flacca, Ononis spinosa*) are present.

pH ($SrCl_2$)

In all transects the soil is slightly alkaline (using the criteria of SCHEFFER & SCHACHTSCHABEL (1976) with values between pH 7.0 and 7.6.

Total available N and P, PO_4^{3-}, NH_4, NO_2^- and NO_3^-.

As the values of total nitrogen and nitrogen compounds show a considerable temporal and spatial variability, comparison of the transects does not result in any conclusion about the difference between them. The same applies for the phosphorus and phosphate values.

C/N ratio

The relatively low C/N ratios indicate a fairly rapid mineralisation. The mean C/N ratio in the top soil of the transects is: Anna

Friso 15 (σ = 1.78, n = 3), Koegat 15 (σ =3.3, n= 4), Cambron 11 (σ =1 n = 4), Vlaamse Kreek 11 (σ =1.5, n = 4).

3.1.2. The vegetation

For general syntaxonomic and synecological information about the communities dealt with here, we refer to WESTHOFF & DEN HELD 1969, SYKORA 1982 a,b and c.

Anna Friso

The vegetation presents a transition downward from a *Lolio-Cynosuretum* into an *Agrostio-Trifolietum fragiferi* and finally into a *Halo-Scirpetum maritimi*. The *Lolio-Cynosuretum* is dominated by *Ononis spinosa* and the *Armerion* element is represented by *Carex distans*, *Juncus gerardi* and *Glaux maritima*.

Vlaamse Kreek

In this transect a species-poor *Lolio-Cynosuretum* occurs in the upper part, adjoining the basal community of *Agrostis stolonifera-*[*Lolio-Potentillion*]. The lowest quadrats are subject to intensive poaching.

Cambron

The upper part of this transect is covered by a *Poo-Lolietum*, which is gradually replaced by the *Nasturtio-Alopecuretum geniculati*.

Koegat

In this transect the sequence is 1) *Poo-Lolietum*, 2) derivate community of *Festuca arundinacea-*[*Lolio-Potentillion*] in its *Alopecurus geniculatus* type and 3) *Halo-Scirpetum maritimi*.

3.2. Vegetation boundaries and vegetation zonation

3.2.1. Anna Friso (table 1 a-c)

3.2.1.1. Floristic composition

In the dendrograms (fig. 6 a-c) four main clusters can be distinguished in 1979 and 1981 and three in 1980. The zones corresponding with these clusters are characterized as follows (tables 1 a-c):

a) the upper zone contains mainly the *Molinio-Arrhenatheretea* species *Cynosurus cristatus, Trifolium pratense, Ononis spinosa, Poa pratensis, Carex flacca , Cerastium fontanum, Festuca rubra, Taraxacum officinale* group; besides *Brachythecium rutabulum, Festuca arundinacea* and less prominent *Prunella vulgaris, Bellis perennis, Ranunculus acris, Lolium perenne, Holcus lanatus, Poa trivialis, Ranunculus bulbosus, Leontodon taraxacoides (Molinio-Arrhenatheretea), Carduus crispus, Cirsium arvense (Artemisietea)* and *Stellaria media (Chenopodietea).*

b) the lowest zone is almost exclusively composed of *Phragmites australis, Scirpus maritimus* and *Scirpus lacustris* ssp. *tabernaemontani (Halo-Scirpetum maritimi).*

c) the middle zone is transitional between the other ones, i.e. it penetrated by species characterizing the upper and lower part of the transect. A vegetation belt thus characterized has been called a boundary zone by VAN DER MAAREL (1976). According to WESTHOFF & VAN LEEUWEN (1966) the contact zones, i.e. border areas between opposite situations (wet-dry, salt-fresh, rich-poor in nutrients etc.) are characterized by their own ecological and phytosociological features (species combination) and differ from those of the adjacent extremes. These authors remarked that the vegetation of such a contact zone does always belong to the *Agropyro-Rumicion.* In case of the transect Anna Friso, the boundary zone is differentiated by *Agrostis stolonifera, Glaux maritima, Juncus gerardi, Trifolium fragiferum* (character- and differential species of the *Agrostio- Trifolietum fragiferi*) and *Drepanocladus aduncus* having a higher cover, while *Centaurium pulchellum, Eleocharis uniglumis (Agrostio-Trifolietum fragiferi)* and *Samolus valerandi* are almost restricted to this part of the transect.

In 1979 and in 1981 the middle zone can be subdivided into two subzones. The upper subzone in which *Trifolium fragiferum* and *Drepanocla-*

ûus aduncus have their highest cover is transitional to the vegetation growing in the upper part of the transect. The lower subzone forms a downward transition. *Eleocharis uniglumis* and *Glaux maritima* have their highest cover in this zone. In 1981 *Samolus valerandi (Halo-Scirpion, Armerion, Lolio-Potentillion* or *Nanocyperion)* and also *Juncus bufonius (Nanocyperion)* were restricted to this sector of the transect.

3.2.1.2. Hydrology

While the upper zone is never inundated (fig.1a), the lower zone, the *Halo-Scirpetum* is continuously submerged throughout most years. This is in accordance with the data of TYLER (1971). From the middle zone the upper subzone is flooded in winter only, the upper quadrats even only in winters with sufficient precipitation. The lower subzone is inundated every year during winter and spring and in years of excessive rainfall even in summer. In 1981 the two subzones are pronounced which is due to the sharper contrast in the inundation length. Whereas the upper subzone is not flooded during the summer season, the lower subzone has been flooded from 8 to 18 weeks (table 1c). For 1979, the occurrence of two subzones in the middle zone is less easily understandable. This might be due to insufficient number of records in that year or to the influence of the subsoil water on the reduction of the root layer in the quadrats 13-15. Whereas the highest quadrat inundated in the summer of 1979 was quadrat 16, the highest quadrat flooded in the year 1980 was number 13. If the influence of the subsoil water on the root layer of the adjoining non-inundated quadrats applies, this impact may be responsible for the absence of a subdivision in this year. Besides the increase in flooding period is considerably more gradual than in the year 1981 which showed a clear subdivision of the middle zone.

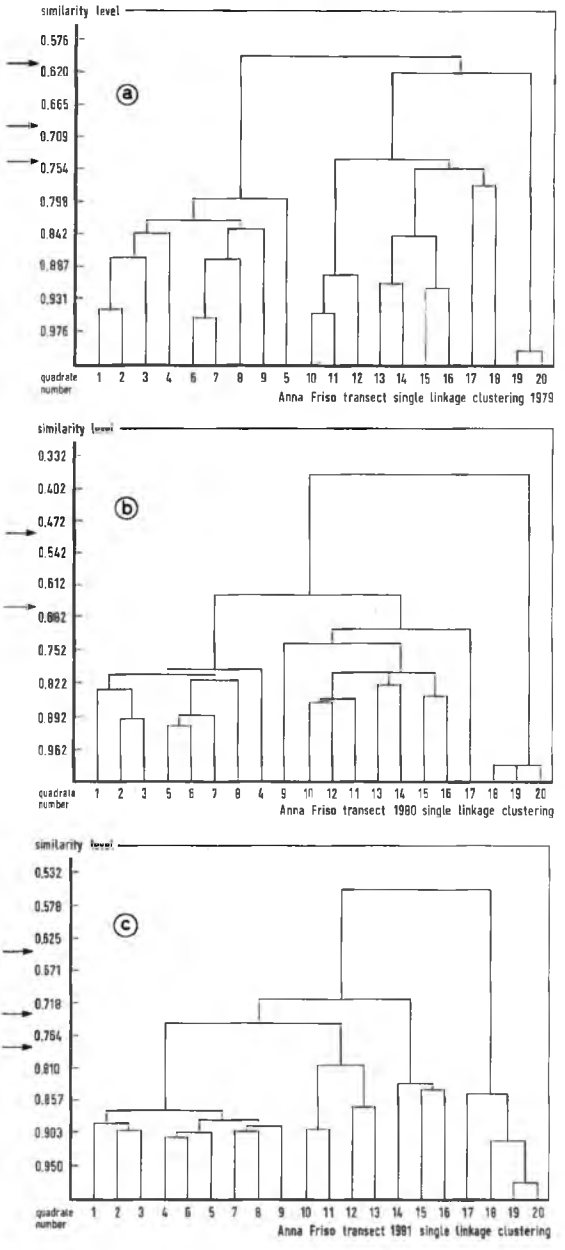


fig.6 Dendrograms derived from single linkage clustering with similarity ratio applied to the data from the transect Anna Friso in the successive years. Threshold values are indicated with an arrow.

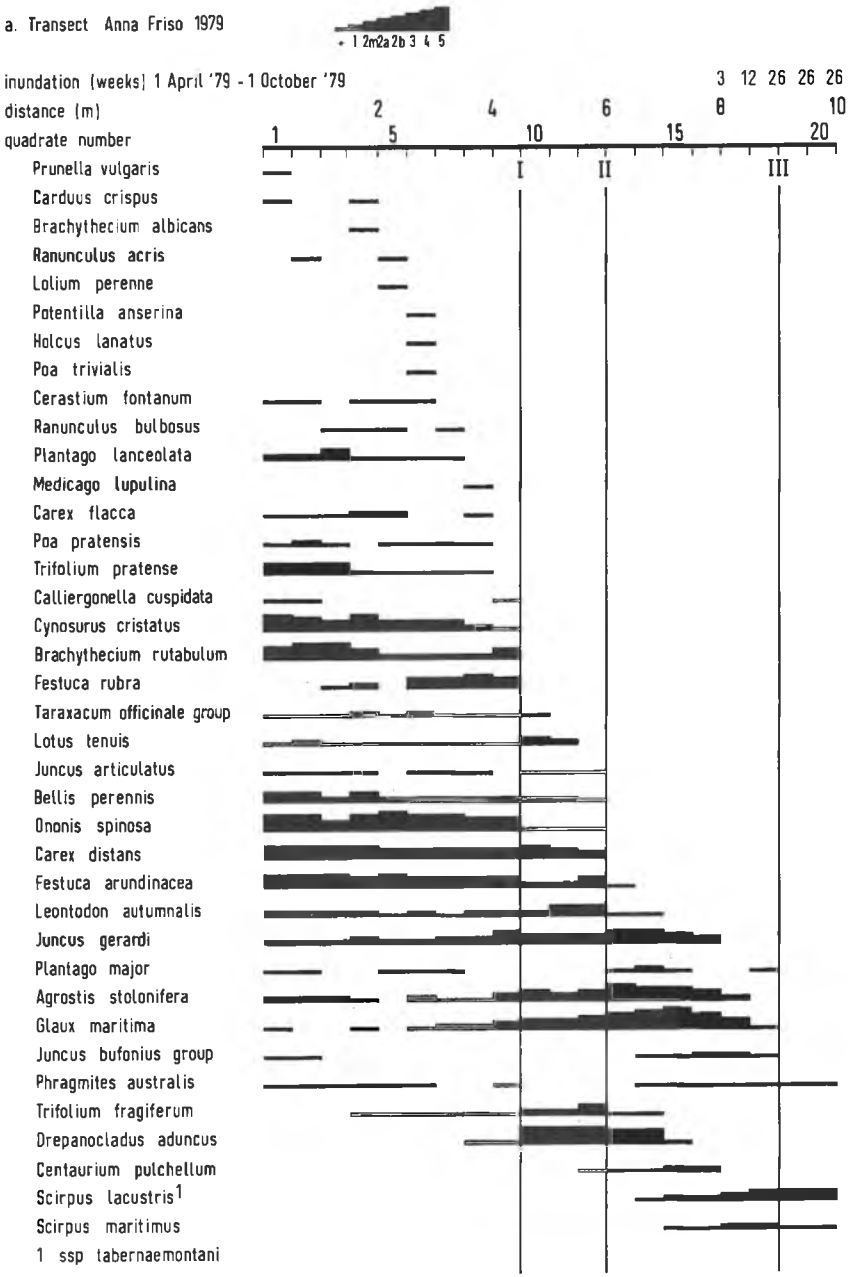


table 1. Anna Friso.Belt transect showing the floristic differentiation of the plant cover in the successive years.For explanation of the dividing lines I, II and III see the text.

b. Transect Anna Friso 1980

inundation (weeks) 1 October '79 – 1 October '80 1 4 6 11 14 21 29 38 41 44 47 51

inundation (weeks) 1 April '80 – 1 October '80 05 3 7 14 15 18 21 26

distance (m) 2 4 6 8 10

quadrate number 1 5 10 15 20

I II

Trifolium repens
Calliergonella cuspidata
Ranunculus acris
Prunella vulgaris
Holcus lanatus
Carduus crispus
Cirsium arvense
Cerastium fontanum
Ranunculus bulbosus
Lolium perenne
Carex flacca
Plantago lanceolata
Trifolium pratense
Brachythecium rutabulum
Festuca rubra
Poa pratensis
Taraxacum officinale group
Cynosurus cristatus
Ononis spinosa
Lotus tenuis
Carex distans
Festuca arundinacea
Juncus articulatus
Plantago major
Trifolium fragiferum
Bellis perennis
Leontodon autumnalis
Agrostis stolonifera
Juncus gerardi
Juncus bufonius group
Glaux maritima
Phragmites australis
Centaurium pulchellum
Drepanocladus aduncus
Samolus valerandi
Eleocharis uniglumis
Veronica catenata
Scirpus lacustris[1]
Scirpus maritimus

1 ssp tabernaemontani

c. Transect Anna Friso 1981

inundation (weeks) 1 October '80 - 1 October '81 0.5 9 15 29 40 44 45 46 46 ?

inundation (weeks) 1 April '81 - 1 October '81 8 15 18 19 20 21 ?

distance (m) 2 4 6 8 10

quadrate number 1 5 10 15 20

I II III

Calliergonella cuspidata
Prunella vulgaris
Leontodon taraxacoides
Poa annua
Poa trivialis
Holcus lanatus
Plantago lanceolata
Cerastium fontanum
Carduus crispus
Cirsium arvense
Stellaria media
Poa pratensis
Trifolium pratense
Carex flacca
Ranunculus acris
Cynosurus cristatus
Brachythecium rutabulum
Bellis perennis
Ononis spinosa
Festuca rubra
Taraxacum officinale group
Carex distans
Leontodon autumnalis
Festuca arundinacea
Trifolium fragiferum
Lotus tenuis
Juncus articulatus
Plantago major
Juncus gerardi
Agrostis stolonifera
Phragmites australis
Glaux maritima
Drepanocladus aduncus
Centaurium pulchellum
Juncus bufonius group
Samolus valerandi
Eleocharis uniglumis
Srirpus maritimus
Scirpus lacustris[1]

1 ssp tabernaemontani

3.2.2. Vlaamse Kreek

3.2.2.1. Floristic composition (table 2 a-c)

From the three main clusters in 1979 only two remain in 1980 and 1981 (fig. 7 a-c and table 2 a-c). The quadrats 19 and 20 are presented as separate relevés in 1979 and 1981. In 1980 quadrat 19 belongs to the cluster formed by the lowest zone.

a) the upper zone is characterized by *Lolium perenne*, *Cynosurus cristatus (Lolio-Cynosuretum)*, *Holcus lanatus*, *Cerastium fontanum (Molinio-Arrhenatheretea)*, *Trifolium fragiferum (Agrostio-Trifolietum fragiferi)*, *Poa annua (Plantaginetea) and Ranunculus repens*.

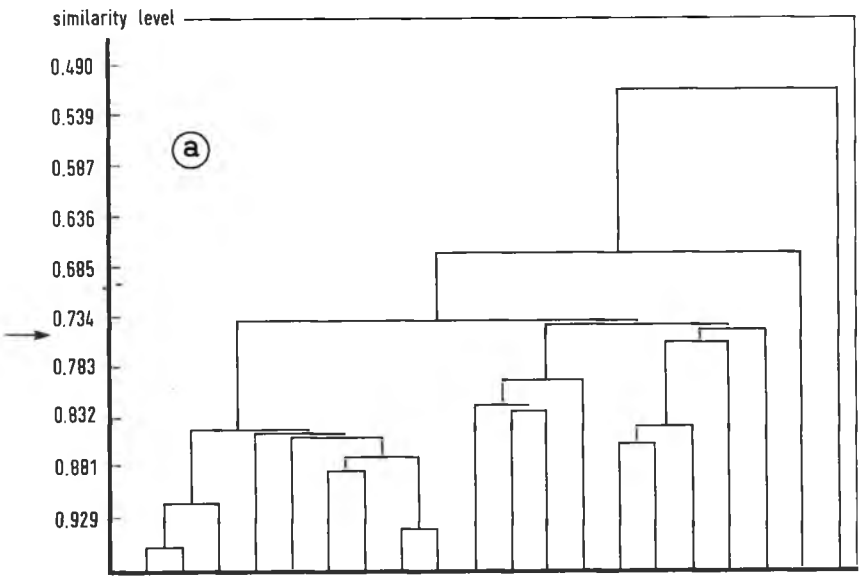
b) the lowest zone is species-poor and both the total vegetation and the individual species have a low coverage. In 1979 and 1981 no species has its main occurrence in this zone. In 1980 however, the year with the summer inundation, it is characterized by *Veronica catenata*, *Rorippa islandica (Bidention)* and by *Phragmites australis* and *Scirpus maritimus (Phragmitetea)*.

c) the middle zone is differentiated by *Agrostis stolonifera*, *Alopecurus geniculatus (Lolio-Potentillion)*, *Potentilla anserina (Plantaginetea)*, *Juncus bufonius (Nanocyperion)* and *Rumex palustris (Bidention)*. *Rorippa islandica* is almost restricted to this zone in 1979 and in 1981, while it is characterizing the lowest zone in 1980 (see above). In 1979 the middle zone is divided into two subzones of which the upper one is transitional to the upper zone.

3.2.2.2. Hydrology (fig.1 b)

Like in the transect Anna Friso most of the quadrats of the upper zone are never inundated. Only the quadrats positioned lower than quadrat 9 are inundated during winter and in 1981 even during a short period (1-2 weeks) in summer (table 2c). The boundary between *Lolio-Potentillion* and *Lolio-Cynosuretum* (upper and middle zone respectively) is clearly visible in the field. In 1979 the altitude of this boundary was measured. The altitudinal variation was only 4 cm varying between -49 and -53 cm, over a total length of 125 m. The horizontality of the line indicates that hydrology is a master factor here.

In 1979 the quadrats 10-13 were inundated till the middle of April. The quadrats 14-18 were flooded till the end of June. Consequently the middle zone has been divided into two subzones of which the upper one is transitional to the upper zone. In 1981 the upper subzone did not appear as a separate cluster; it was then joined with the upper zone. Although, like in 1979, these quadrats ran dry in the middle of April, the total inundation period was considerably shorter. In the summer of 1979 the quadrats 11-13 were flooded for about 8 weeks, in the summer of 1981 inundation lasted about 1-2 weeks.
In 1980 the quadrats 11-13 were combined with the middle zone. Although winter inundation of these quadrats lasted till the end of February only, all these quadrats were once again flooded during the month of July, in the middle of the growing season. This summer inundation also caused the quadrats 17 and 18 to shift to the lower zone of the dendrogram. Unlike the lowest zone of the transect Anna Friso, the lowest zone of the Vlaamse Kreek is not flooded continuously, although the period of inundation is much longer compared to that of the middle zone. The soft, waterlogged soil in combination with severe poaching results in a considerable decrease in plant cover.



Vlaamse Kreek transect 1979 single linkage clustering

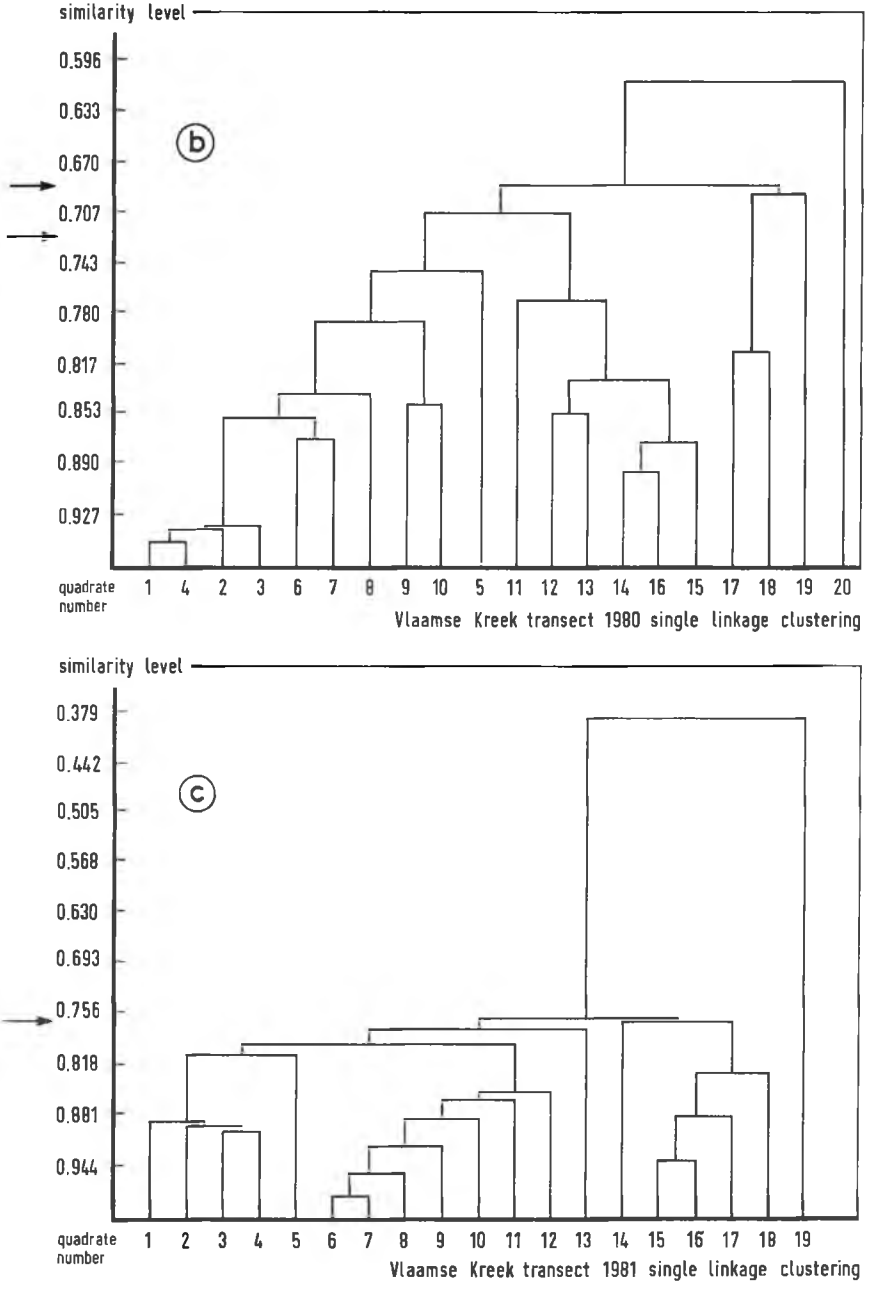
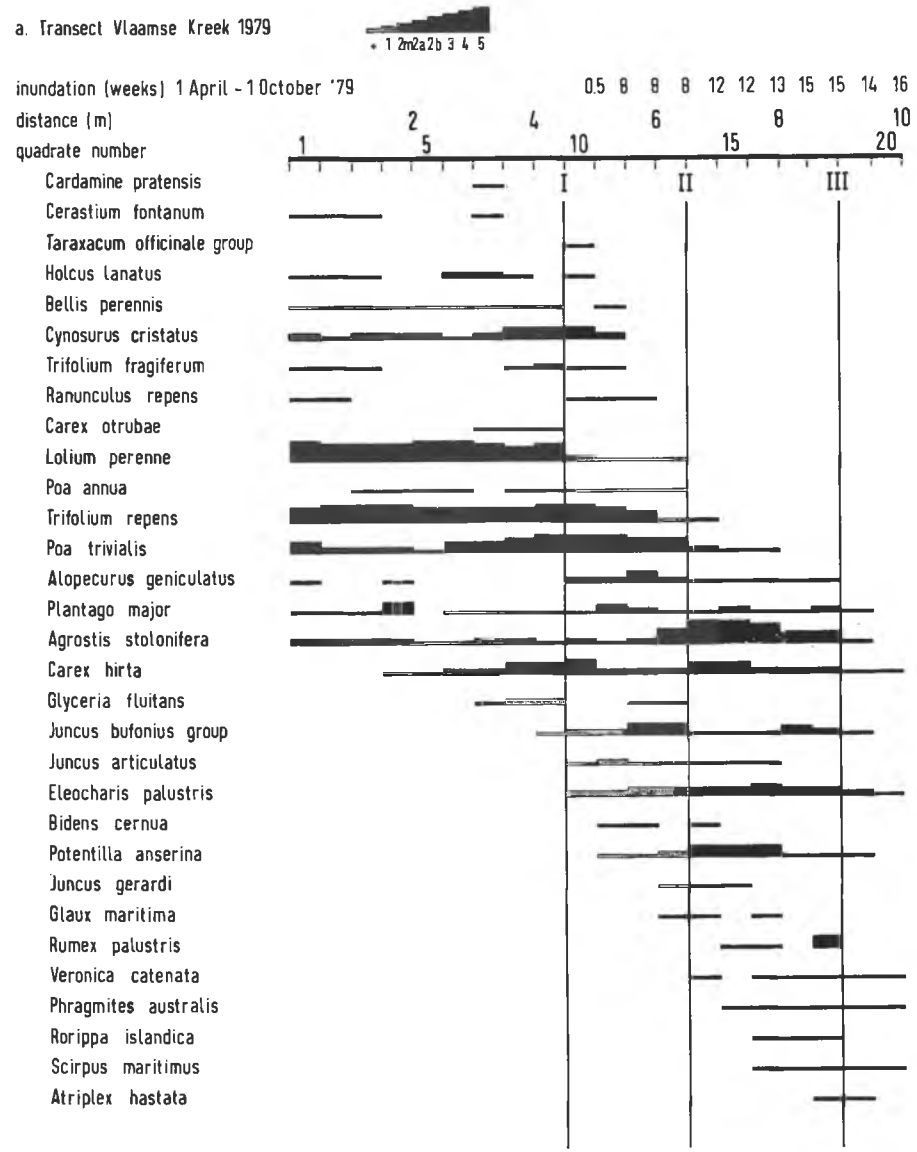
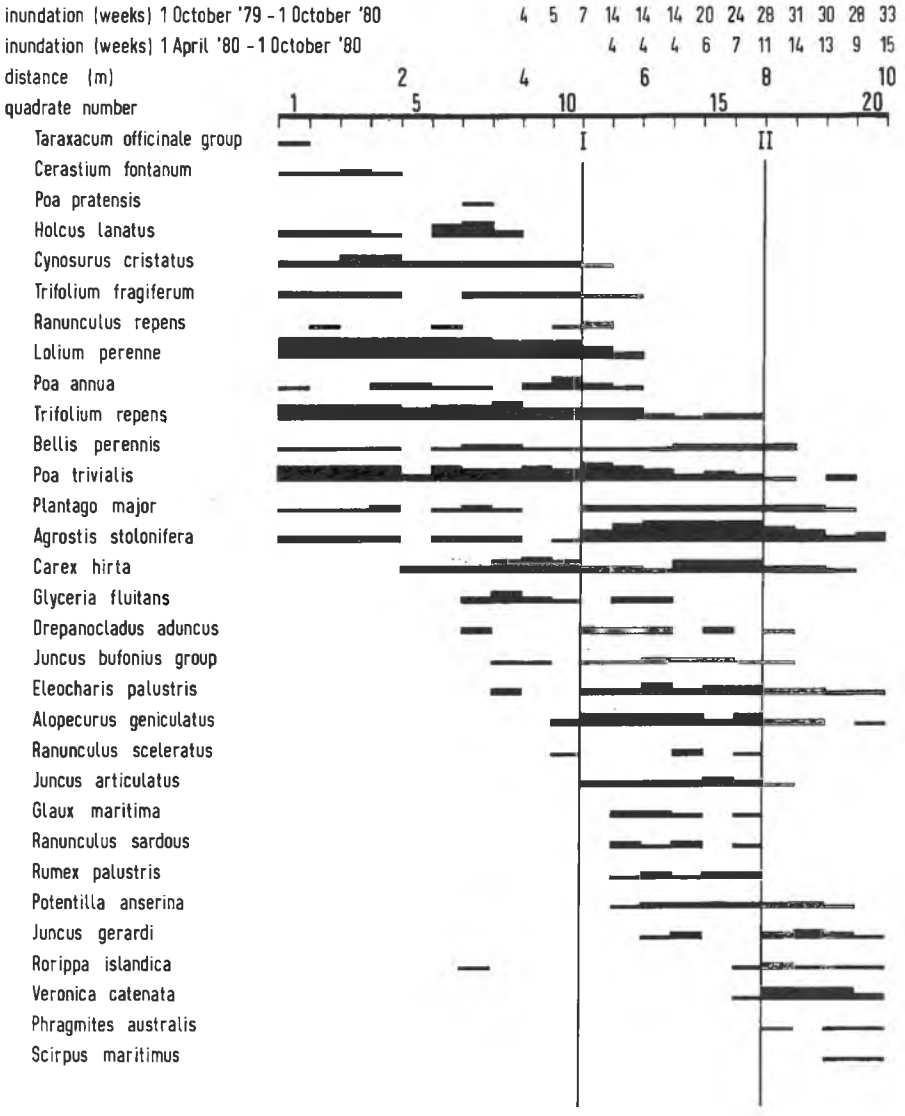


fig.7 Dendrograms of the transect Vlaamse Kreek in the successive years. (see fig.6).

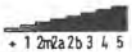
Table 2. Vlaamse Kreek. Belt transect, see table 1.

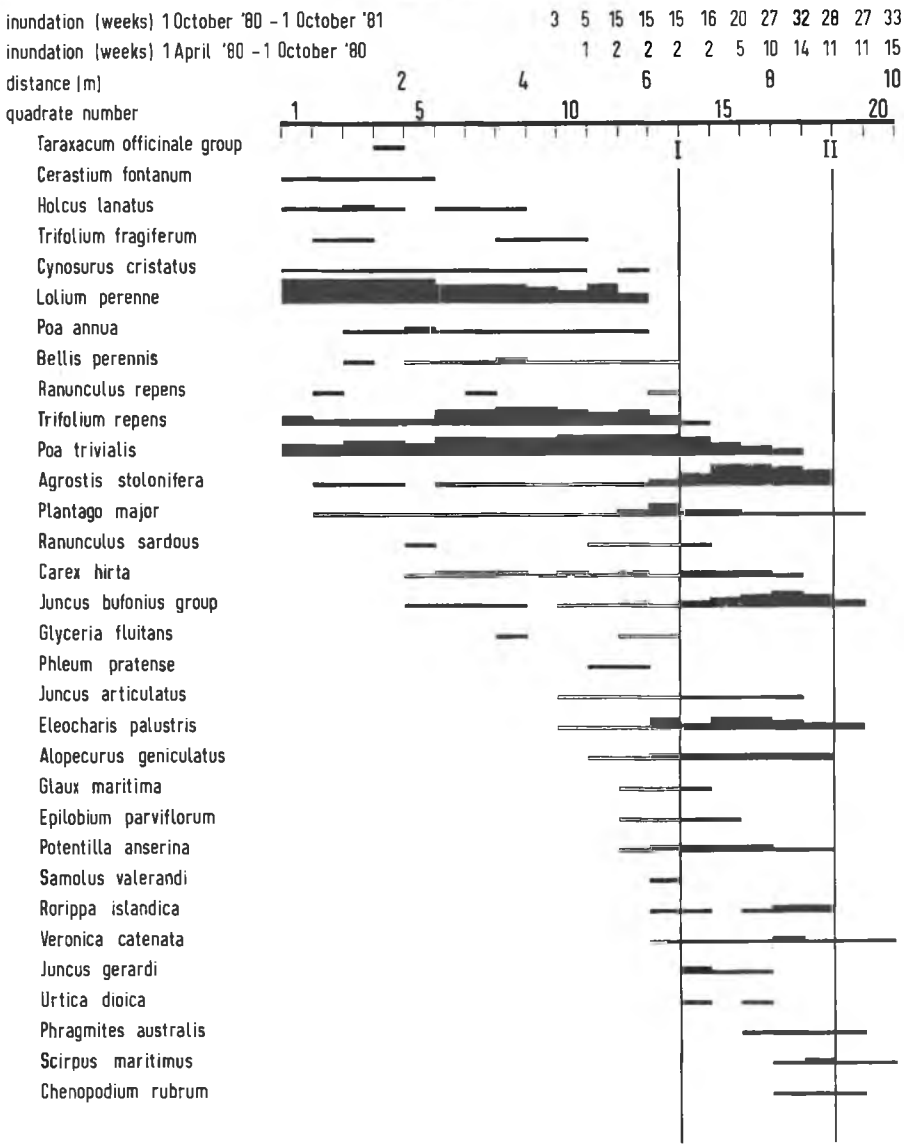


b. Transect Vlaamse Kreek 1980



c. Transect Vlaamse Kreek 1981





3.2.3. Cambron

3.2.3.1. Floristic composition (table 3 a-c)

In this transect the zonation is obscure and the transitions are gradual. *Glyceria declinata*, a species indicative for wet places, is occurring throughout the transect. The same applies for the *Lolio-Potentillion* species *Agrostis stolonifera* and *Alopecurus geniculatus*. Although very similar to each other (about 86 %) two main clusters can be distinguished in 1979, with the main division between the quadrats 32 and 33 (fig. 8a). For the year 1980 it is impossible to distinguish main clusters (fig. 8b). Line I drawn in table 3b has not been derived from the dendrogram, but has been based on fig. 1c. It divides the table into a flooded and a non-flooded part. In 1981 the dendrogram (fig. 8c) indicates two main clusters with the division between the quadrats 30 and 31.

a) species restricted to or differentiating the upper zone are *Lolium perenne, Polygonum aviculare (Plantaginetea), Ranunculus sardous (Nasturtio-Alopecuretum geniculati), Poa trivialis, Cerastium fontanum, Festuca pratensis, Poa pratensis (Molinio-Arrhenatheretea), Stellaria media (Chenopodietea), Chamomilla recutita (Secalietea), Urtica dioica* and *Elymus repens*.

b) the lower zone is differentiated by *Nasturtium microphyllum, Juncus inflexus (Lolio-Potentillion), Veronica catenata, Bidens cernua (1981), Rumex maritimus (Bidention), Eleocharis palustris, Scirpus lacustris, Alisma plantago-aquatica, Oenanthe aquatica, Mentha aquatica, Scirpus maritimus (Phragmitetea, Halo-Scirpetum), Drepanocladus aduncus* and *Juncus articulatus*. *Glyceria declinata*, although occurring throughout the transect, is clearly increasing downward. The coverage of *Alopecurus geniculatus (Lolio-Potentillion)* is highest in the middle of the transect.

3.2.3.2. Hydrology

The gradual transition in the species composition from the upper into the lower zone corresponds to the hydrological conditions. The downward increase of the flooding period is very gradual. Although the

first 20 quadrats are never inundated (fig.1 c) the water level remains close to the soil surface (fig.2 c) and the soil is waterlogged throughout the greater part of the year. During periods of high rainfall the water level follows the profile of the transect (fig.3 c). This is probably a consequence of the soil's texture. While the soil of the transects Anna Friso and Vlaamse Kreek consists of respectively sand or loamy sand, the soil of the Cambron transect is composed of sandy loam to sandy clay loam with a higher soil water retention capacity. The independence of the water level in the transect from that in the nearby ditch indicates that stagnation is an important process in the hydrology of this transect. Because of these hydrological characteristics the period during which the top soil is fully waterlogged gradually increases downward. The lowest quadrats located in the middle of the creek are flooded almost throughout the year (fig. 1c).

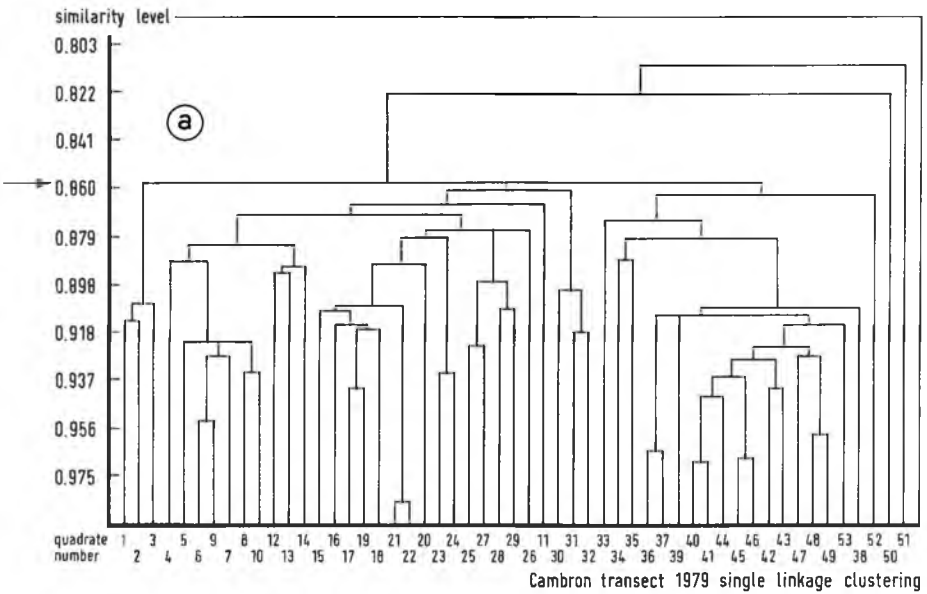
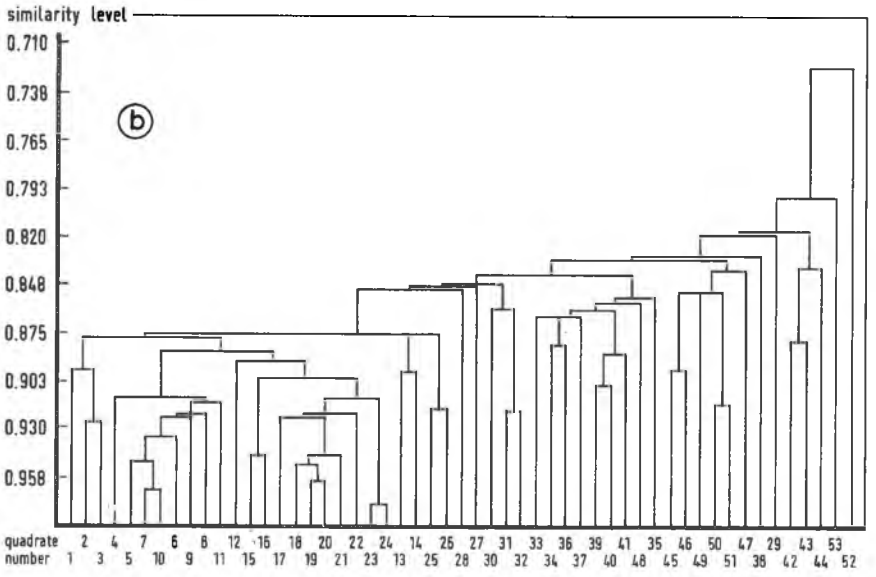
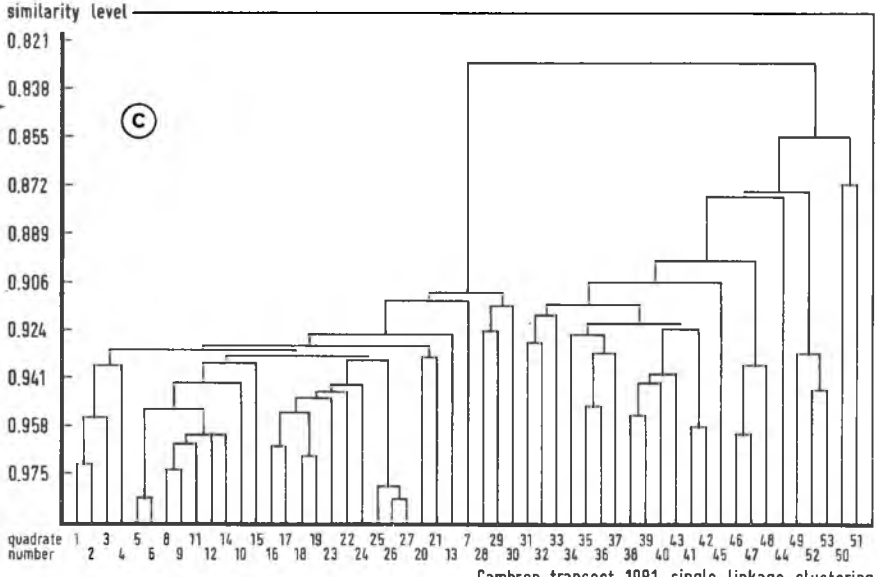


fig.8 Dendrograms of the transect Cambron in the successive years (see fig.6).

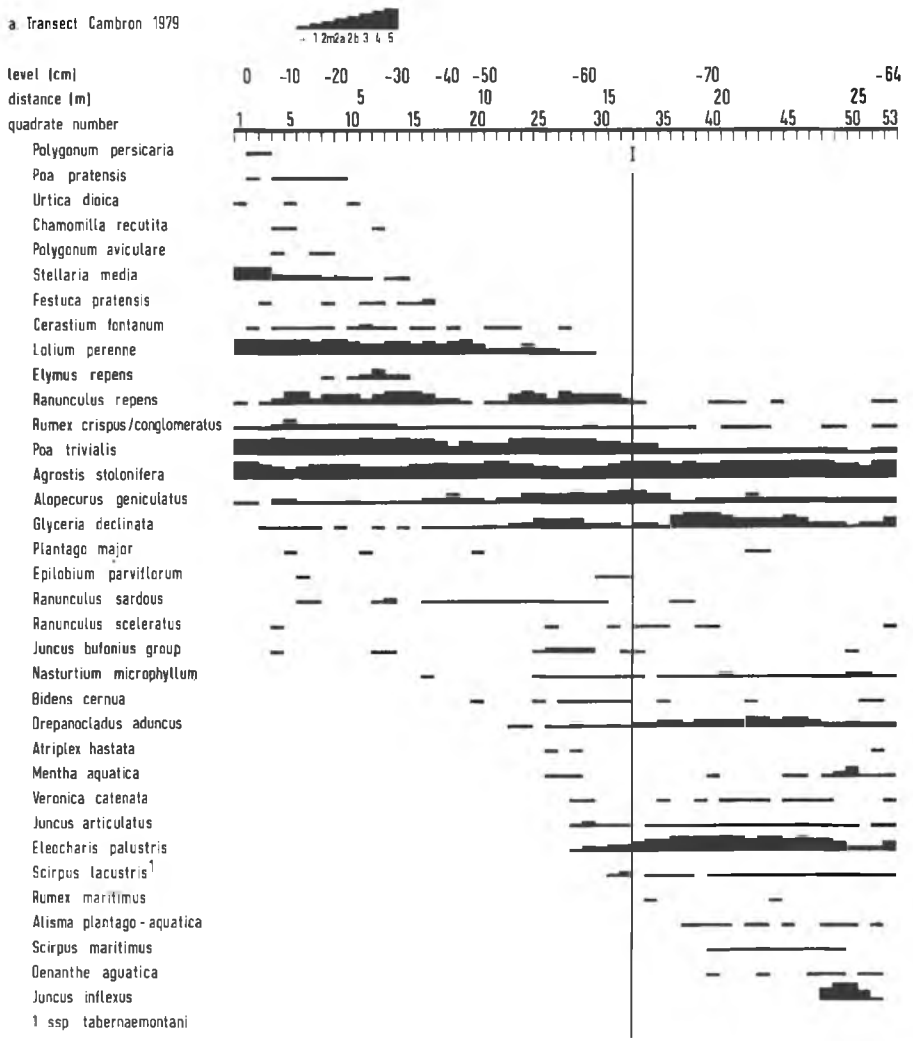


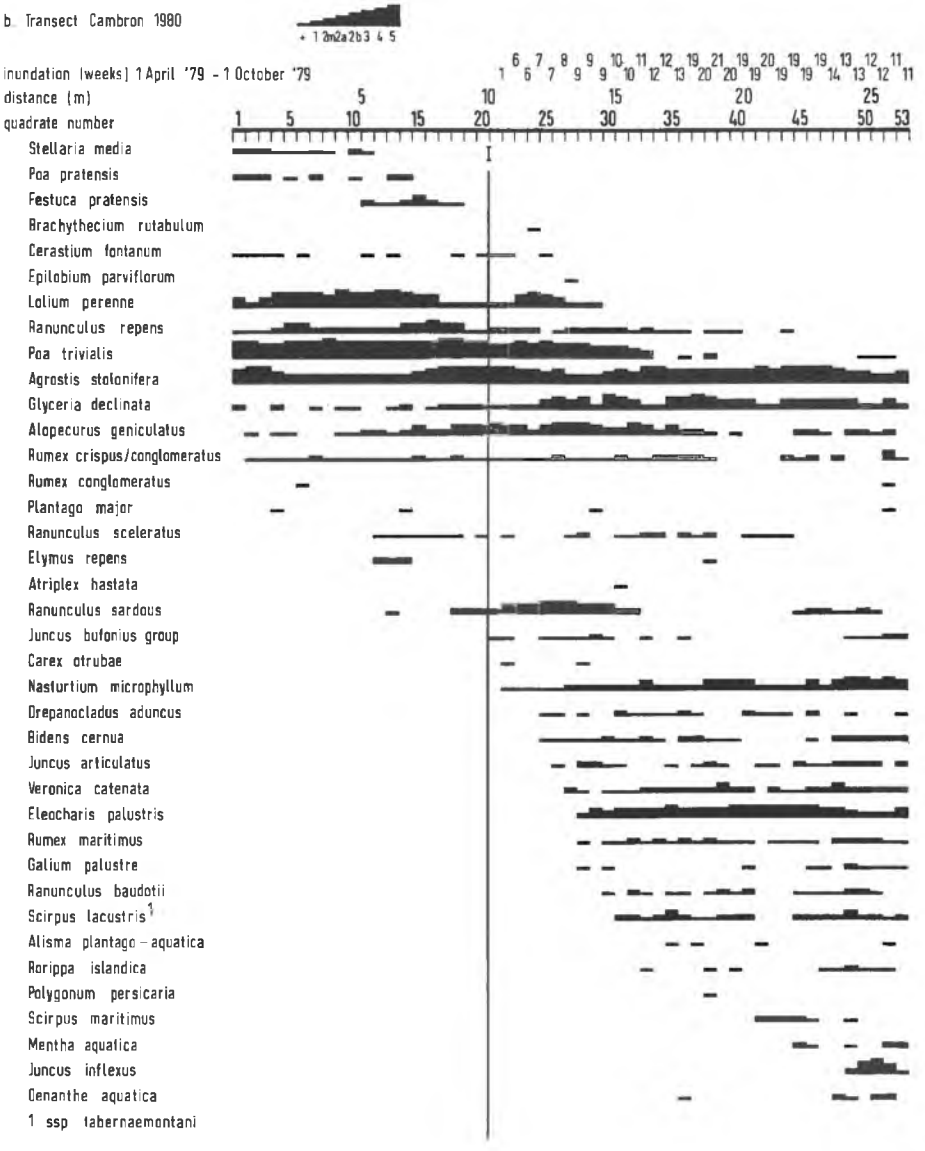
Cambron transect 1980 single linkage clustering

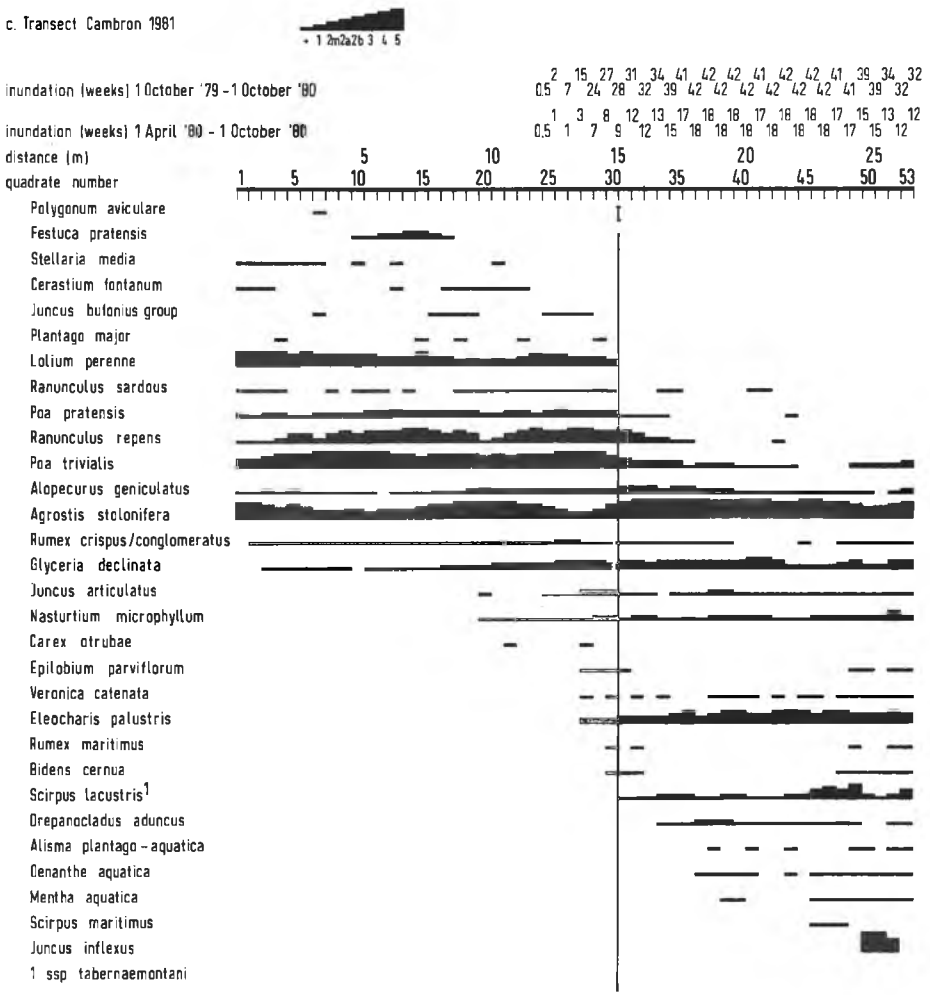


Cambron transect 1981 single linkage clustering

Table 3 Cambron. Belt transect, see table 1.




b. Transect Cambron 1980
+ 1 2m 2a 2b 3 4 5
inundation (weeks) 1 April '79 - 1 October '79
1 6 6 7 7 8 9 9 9 10 10 11 12 12 13 19 20 21 20 19 20 19 19 19 14 13 13 12 12 11 11
distance (m)
5 10 15 20 25
quadrate number
1 5 10 15 20 25 30 35 40 45 50 53
Stellaria media
Poa pratensis
Festuca pratensis
Brachythecium rutabulum
Cerastium fontanum
Epilobium parviflorum
Lolium perenne
Ranunculus repens
Poa trivialis
Agrostis stolonifera
Glyceria declinata
Alopecurus geniculatus
Rumex crispus/conglomeratus
Rumex conglomeratus
Plantago major
Ranunculus sceleratus
Elymus repens
Atriplex hastata
Ranunculus sardous
Juncus bufonius group
Carex otrubae
Nasturtium microphyllum
Drepanocladus aduncus
Bidens cernua
Juncus articulatus
Veronica catenata
Eleocharis palustris
Rumex maritimus
Galium palustre
Ranunculus baudotii
Scirpus lacustris[1]
Alisma plantago - aquatica
Rorippa islandica
Polygonum persicaria
Scirpus maritimus
Mentha aquatica
Juncus inflexus
Oenanthe aquatica
1 ssp tabernaemontani


c. Transect Cambron 1981
+ 1 2m2a2b 3 4 5
inundation (weeks) 1 October '79 - 1 October '80
2 15 27 31 34 41 42 42 41 42 42 41 39 34 32
0.5 7 24 28 32 39 42 42 42 42 42 42 41 39 32
inundation (weeks) 1 April '80 - 1 October '80
1 3 8 12 13 17 18 18 18 17 18 18 17 15 13 12
0.5 1 7 9 12 15 18 18 18 18 18 18 17 15 12
distance (m)
5 10 15 20 25
quadrate number
1 5 10 15 20 25 30 35 40 45 50 53
Polygonum aviculare
Festuca pratensis
Stellaria media
Cerastium fontanum
Juncus bufonius group
Plantago major
Lolium perenne
Ranunculus sardous
Poa pratensis
Ranunculus repens
Poa trivialis
Alopecurus geniculatus
Agrostis stolonifera
Rumex crispus/conglomeratus
Glyceria declinata
Juncus articulatus
Nasturtium microphyllum
Carex otrubae
Epilobium parviflorum
Veronica catenata
Eleocharis palustris
Rumex maritimus
Bidens cernua
Scirpus lacustris[1]
Drepanocladus aduncus
Alisma plantago-aquatica
Oenanthe aquatica
Mentha aquatica
Scirpus maritimus
Juncus inflexus
1 ssp tabernaemontani

3.2.4. Koegat

3.2.4.1. Floristic composition (table 4 a-c).

Like in the Cambron the zonation in the Koegat transect is unclear and the transitions are gradual (table 4 a-c). In 1979 and 1981 the lower quadrats (47)48 to and including 75 form one cluster (fig.9 a and c). The similarity with the cluster formed by the quadrats 1-46(47) is very high, indicating the gradualness of the transition. In 1980 the line (fig.9 b) between quadrat 48 and 49 is indicated because it corresponds to the highest water level.

a) the upper zone is differentiated by *Festuca pratensis, Poa trivialis, Cerastium fontanum, Holcus lanatus (Molinio-Arrhenatheretea), Lolium perenne (Plantaginetea), Alopecurus geniculatus, Trifolium fragiferum (Lolio-Potentillion), Ranunculus repens* and *Elymus repens.*

b) the lower zone is differentiated by *Scirpus lacustris* ssp. *tabernaemontani, Juncus gerardi, Glaux maritima, Scirpus maritimus, Phragmites australis (Halo-Scirpetum maritimi)* and by *Atriplex hastata* and *Chenopodium rubrum (Bidention). Eleocharis uniglumis (Lolio-Potentillion)* occurs over the whole range of the transect but has its lowest occurrence in the upper part and the highest cover values in the middle of the transect. The same applies for *Plantago major, Potentilla anserina (Plantaginetea), Festuca arundinacea* (differential species of the derivate community of *Festuca arundinacea-*[*Lolio-Potentillion*], *Agrostis stolonifera, Carex otrubae (Lolio-Potentillion), Ranunculus sardous Ranunculus sceleratus* (except in 1981) and *Epilobium parviflorum* (character- and differential species of the *Nasturtio-Alopecuretum geniculati).*

3.2.4.2. Hydrology

The transect Koegat is flooded less frequently and the duration of the inundation is shorter compared to the other transects (fig.1d). The cluster of quadrats forming the lower zone was totally inundated during periods with the highest water level (see fig. 1 d 1980). At these moments the water-line corresponds approximately with quadrat 48.

No flooding of the higher located quadrats has been observed. While in 1979 the water level did not raise above quadrat 64, the transect was not flooded at all in 1981. Like in the Cambron the top soil of the Koegat is waterlogged during a great part of the year even in the highest quadrats. It consists of loam to clay loam and the vertical flow of water is impeded by a peat layer parallel to the surface at a depth of 35-70 cm (fig.10). Consequently the water level is close to the soil surface (less than 30 cm) during the greater part of the year (fig. 2d and 3d), the deepest water level measured being 47 cm. Because of these hydrological conditions the drier habitats are missing and thus vegetation change is almost continuous, forming an ecosyncline (VAN DER MAAREL 1976, VAN DER MAAREL & WESTHOFF 1964). Such a zonation in which the species characteristic of certain levels are mixed together is called a diffuse zonation by KOPECKY (1969).

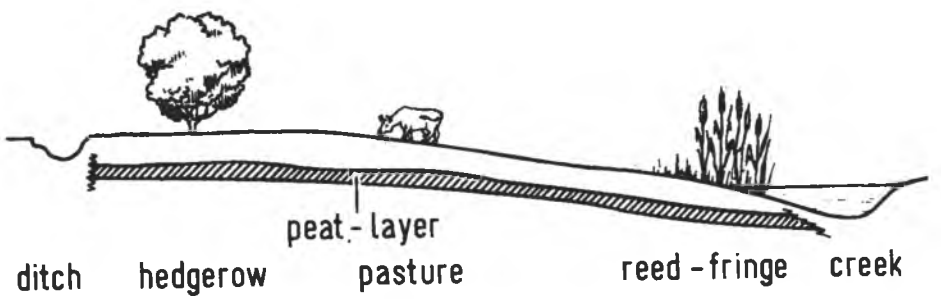


fig. 10 Topographical drawing of the transect Koegat.

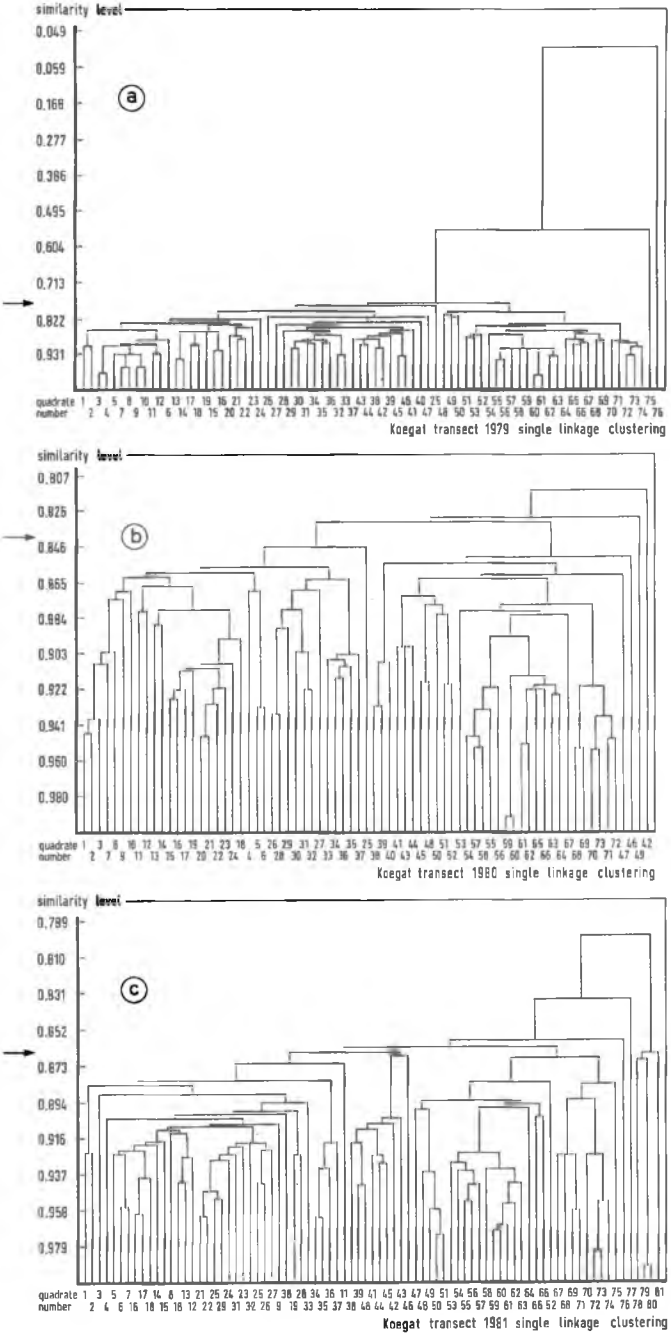


fig.9 Dendrograms of the transect Koegat in the successive years (see fig.6).

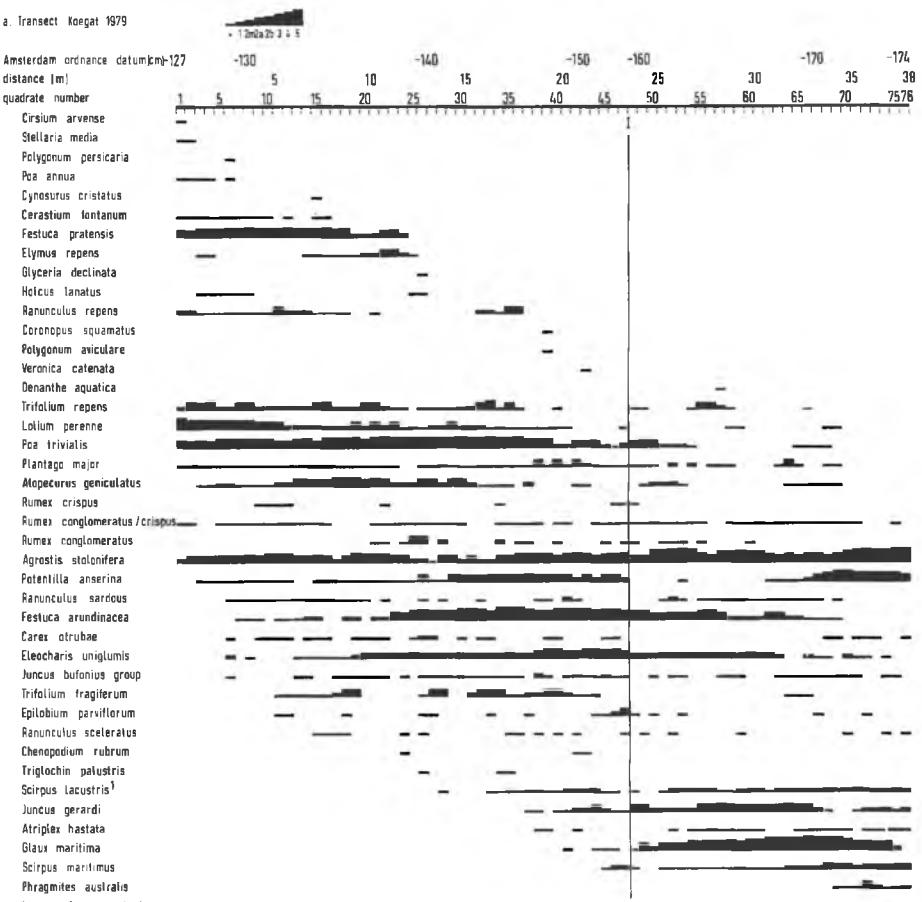
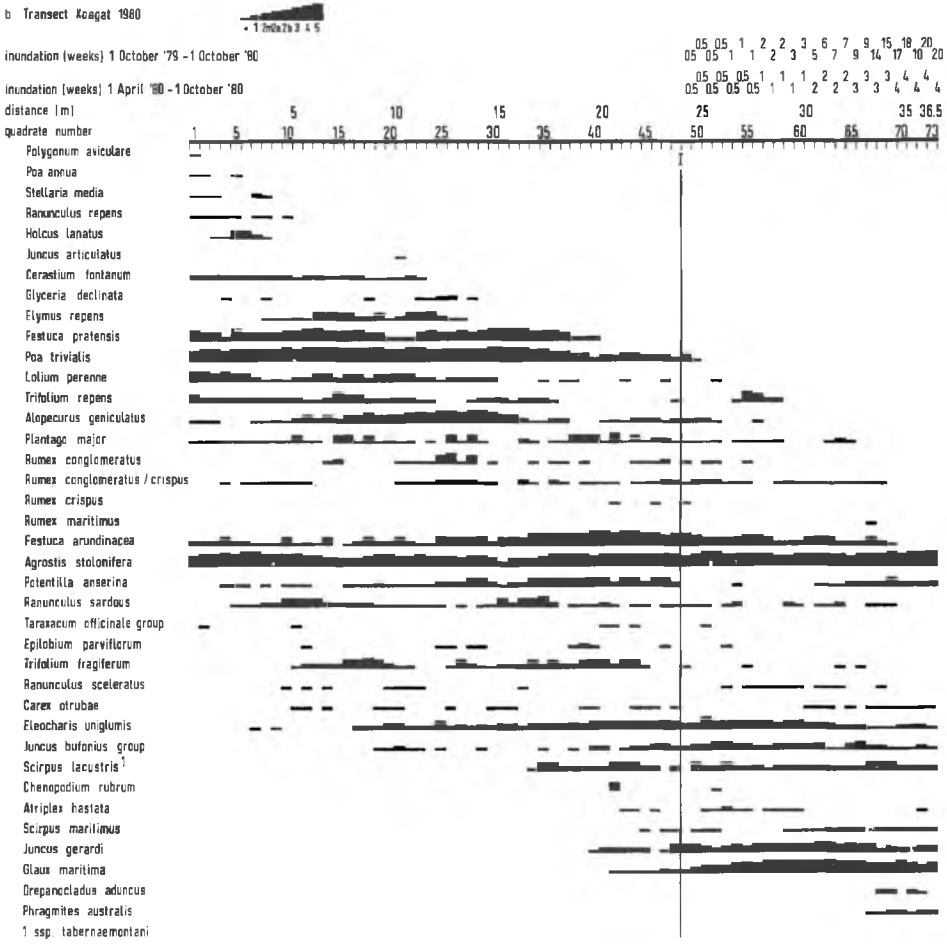


table 4. Koegat.Belt transect, see table 1.


b Transect Koagat 1980
inundation (weeks) 1 October '79 - 1 October '80
inundation (weeks) 1 April '80 - 1 October '80
distance (m)
quadrate number
Polygonum aviculare
Poa annua
Stellaria media
Ranunculus repens
Holcus lanatus
Juncus articulatus
Cerastium fontanum
Glyceria declinata
Elymus repens
Festuca pratensis
Poa trivialis
Lolium perenne
Trifolium repens
Alopecurus geniculatus
Plantago major
Rumex conglomeratus
Rumex conglomeratus / crispus
Rumex crispus
Rumex maritimus
Festuca arundinacea
Agrostis stolonifera
Potentilla anserina
Ranunculus sardous
Taraxacum officinale group
Epilobium parviflorum
Trifolium fragiferum
Ranunculus sceleratus
Carex otrubae
Eleocharis uniglumis
Juncus bufonius group
Scirpus lacustris [1]
Chenopodium rubrum
Atriplex hastata
Scirpus maritimus
Juncus gerardi
Glaux maritima
Orepanocladus aduncus
Phragmites australis
1 ssp. tabernaemontani

3.3. Ecotopic fluctuation

The fluctuation of the water level in the creeks is caused by seasonal differences in precipitation and evaporation. In average years precipitation exceeds evaporation during the period from September till March and consequently the transects become flooded. From March till September the water level drops due to the precipitation deficit (fig. 11d). In both 1979 and 1981 the period of precipitation deficit was continuous (fig. 11a and c). However in 1980 the month of July was very cold and wet, resulting in a considerable surplus in net precipitation (fig.11b), and a consequent rise of the water level in the creeks. Flooding during the summer i.e. during the period of maximum growth, can be detrimental to grassland species. The damage is proportional to 1) the sensitivity of the species for flooding; 2) the temperature of the water; 3) the depth of the water and 4) the duration of the flooding. The damage is caused by oxygen depletion mainly resulting from the high consumption of oxygen needed for the decomposition of the submerged organic material (KLAPP 1965,1971). The effect of the fluctuations in water level over the years 1979-1981 on the vegetation of the combined transects is summarized below (see also table 5). For the floristic composition of the zones dealt with beneath see section 3.2.

a. *Upper zone*

In this section species, showing a change in at least one transect and remaining equal in the other ones, are classified according to their increase or decrease in the years studied. The syntaxonomic position is indicated after the species. *LP = Lolio-Potentillion, Ph = Phragmitetea, Arr = Arrhenatherion, MA = Molinio-Arrhenatheretea, Bi = Bidention, Pl = Plantaginetea, As = Asteretea tripolii, Art = Artemisietea, IN = Isoeto-Nanojuncetea, Sec = Secalietea, CB = Callitricho-Batrachion, Chen = Chenopodietea, Mes = Mesobromion.*

increasing from 1979 to 1980

Alopecurus geniculatus LP
Bellis perennis Arr
Brachythecium rutabulum
Carduus crispus Art
Carex distans As
Carex flacca MA
Cerastium fontanum MA
Cirsium arvense Art
Eleocharis palustris Ph
Festuca arundinacea
Festuca pratensis Arr
Glaux maritima As
Glyceria declinata
Holcus lanatus MA
Juncus articulatus
Lotus tenuis As
Nasturtium microphyllum Ph
Ononis spinosa Mes
Phragmites australis Ph
Plantago lanceolata MA
Plantago major Pl
Poa pratensis MA
Poa trivialis MA
Ranunculus sardous LP
Ranunculus sceleratus Bi
Rumex maritimus Bi
Scirpus lacustris ssp. *tabernaemontani Ph*
Taraxacum officinale group Arr

Trifolium fragiferum LP
Trifolium pratense MA
Veronica catenata Bi

decreasing from 1980 to 1981

Agrostis stolonifera LP
Alopecurus geniculatus LP
Bellis perennis Arr
Bidens cernua Bi
Carex hirta LP
Carex otrubae LP
Chenopodium rubrum Bi
Cynosurus cristatus Arr
Drepanocladus aduncus
Eleocharis palustris Ph
Eleocharis uniglumis LP
Elymus repens
Festuca arundinacea
Festuca pratensis Arr
Glyceria fluitans Ph
Juncus bufonius group IN
Leontodon autumnalis Arr
Lolium perenne Pl
Lotus tenuis As
Phragmites australis Ph
Plantago lanceolata MA
Plantago major Pl
Potentilla anserina Pl
Ranunculus bulbosus
Ranunculus sardous LP
Ranunculus sceleratus Bi
Rumex maritimus Bi
Scirpus lacustris ssp. *tabernaemontani Ph*
Taraxacum officinale group Arr
Trifolium fragiferum LP
Trifolium pratense MA
Veronica catenata Bi

decreasing from 1979 to 1980

Carex otrubae LP
Cynosurus cristatus Arr
Drepanocladus aduncus
Eleocharis uniglumis LP
Epilobium parviflorum Ph
Festuca rubra MA
Juncus bufonius group IN
Juncus gerardi As
Chamomilla recutita Sec
Mentha aquatica Ph
Polygonum aviculare Pl
Potentilla anserina Pl
Ranunculus repens
Rumex crispus/conglomeratus
Trifolium repens Arr
Urtica dioica Art

increasing from 1980 to 1981

Atriplex hastata
Brachythecium rutabulum
Festuca rubra MA
Juncus gerardi As
Ranunculus acris MA
Ranunculus repens

A few species (3 in 1980 and 7 in 1981) showed contrasting behaviour in different transects.

b) *Middle zone*

increasing from 1979 to 1980

Agrostis stolonifera LP
Alopecurus geniculatus LP
Carex distans As
Centaurium pulchellum IN
Drepanocladus aduncus
Eleocharis uniglumis LP
Festuca arundinacea
Glaux maritima As
Glyceria fluitans Ph
Leontodon autumnalis Arr
Lolium perenne Pl
Lotus tenuis As

decreasing from 1980 to 1981

Agrostis stolonifera LP
Alopecurus geniculatus LP
Bellis perennis Arr
Centaurium pulchellum IN
Drepanocladus aduncus
Juncus bufonius IN
Leontodon autumnalis Arr
Lotus tenuis As
Phragmites australis Ph
Rumex palustris Bi
Samolus valerandi
Trifolium fragiferum LP

Phragmites australis Ph
Plantago major Pl
Ranunculus sardous LP
Rumex palustris Bi
Samolus valerandi
Scirpus lacustris ssp.*tabernae-montani* Ph
Trifolium fragiferum LP

decreasing from 1979 to 1980	increasing from 1980 to 1981
no species	*Eleocharis uniglumis* LP
	Festuca rubra MA
	Poa trivialis MA

In 1980 *Juncus bufonius* decreased in the Vlaamse Kreek and increased in the transect Anna Friso.

c. *Lower zone*

increasing from 1979 to 1980	decreasing from 1980 to 1981
Bidens cernua Bi	*Alopecurus geniculatus* LP
Carex otrubae LP	*Bidens cernua* Bi
Eleocharis uniglumis LP	*Carex hirta* LP
Galium palustre Ph	*Carex otrubae* LP
Juncus articulatus	*Galium palustre* Ph
Juncus bufonius group IN	*Nasturtium microphyllum* Ph
Juncus gerardi As	*Phragmites australis* Ph
Nasturtium microphyllum Ph	*Potentilla anserina* Pl
Ranunculus baudotii CB	*Ranunculus baudotii* CB
Ranunculus sardous LP	*Ranunculus sardous* LP
Ranunculus sceleratus Bi	*Ranunculus sceleratus* Bi
Rorippa islandica Bi	*Rorippa islandica* Bi
Rumex crispus/conglomeratus	*Rumex crispus/conglomeratus*
Rumex maritimus Bi	*Rumex maritimus* Bi
Scirpus lacustris ssp. *taber-naemontani* Ph	*Trifolium repens* Arr
	Veronica catenata Bi
Veronica catenata Bi	

decreasing from 1979 to 1980	increasing from 1980 to 1981
Alisma plantago-aquatica Ph	*Alisma plantago-aquatica Ph*
Atriplex hastata	*Chenopodium rubrum Bi*
Eleocharis palustris Ph	*Eleocharis palustris Ph*
Epilobium parviflorum Ph	*Epilobium parviflorum Ph*
Glaux maritima As	*Festuca arundinacea*
Juncus inflexus LP	*Lolium perenne Pl*
Lolium perenne Pl	*Oenanthe aquatica Ph*
Phragmites australis Ph	*Poa pratensis MA*
Potentilla anserina Pl	*Poa trivialis MA*
Scirpus maritimus Ph	*Trifolium fragiferum LP*

A few species (4 in 1980 and 7 in 1981) showed contrasting behaviour in different transects.

Table 5 a-d (see following pages). Comparison of the sum of the transformed cover-abundance values of the species and the number of quadrats occupied by every species between the years studied. Σ c= sum of the transformed cover-abundance values, n.q. = number of occupied quadrats, Δc = difference of cover-abundance , + = increase, - = decrease, Δq = difference in number of occupied quadrats.

3.4. Species distribution in relation to the period of submersion.

In this section the species are arranged according to the maximum number of weeks during which the lowest quadrat containing the species concerned, has been flooded in the summer period. For the perennial species the sequence indicates the degree of their tolerance to inundation. As therophytes have the opportunity to complete their whole life cycle within one favourable growing period and as they die after seed production, their presence in the lower quadrats does not necessarily mean that these species are inundation-tolerant. Nevertheless their regenerative strategy enables these species to occur on the above mentioned sites. The species can be classified as follows (for explanation of the abbreviations see 3.3.):

a) species occurring exclusively on non-inundated sites:

Brachythecium albicans
Cardamine pratensis MA
Calliergonella cuspidata
Carduus crispus Art
Chamomilla recutita Sec
Cirsium arvense Art
Elymus repens
Festuca pratensis Arr
Leontodon taraxacoides MA
Medicago lupulina Arr
Plantago lanceolata MA
Polygonum aviculare Pl
Prunella vulgaris MA
Ranunculus acris MA
Ranunculus bulbosus Arr
Stellaria media Chen
Trifolium pratense MA

b) species not flooded in the growing season (1 April- 1 October) but inundated during a short period in winter. The duration in weeks is indicated after the name of the species.

Festuca rubra MA	*0-1*
Carex flacca MA	*0-6*
Cerastium fontanum MA	*0-7*
Poa pratensis MA	*0-11*
Ononis spinosa Arr(Mes)	*0-11*

c) species inundated in both the summer and the winter period. The period of summer inundation is indicated after the species; the inundation during this summer as well as the preceding winter is indicated as ( ); > = more than.

Holcus lanatus MA	*0-0.5*	*(0-4)*
Taraxacum officinale group Arr	*0-0.5*	*(0-15)*
Carex distans As	*0-0.5*	*(0-15)*
Festuca arundinacea	*0-4*	*(0-21)*
Poa annua Pl	*0-8*	*(0-15)*
Cynosurus cristatus Arr	*0-8*	*(0-15)*
Trifolium fragiferum LP	*0-8*	*(0-29)*
Lotus tenuis As	*0-8*	*(0-29)*
Carex otrubae LP	*0-9*	*(0->26)*
Lolium perenne Pl	*0-9*	*(0-28)*
Trifolium repens Arr	*0-12*	*(0-28)*
Chenopodium rubrum Bi	*0-14*	*(0-32)*
Bellis perennis Arr	*0-14*	*(0-38)*
Leontodon autumnalis Arr	*0-14*	*(0-38)*
Atriplex hastata Bi	*0-15*	*(0-20)*
Rumex palustris Bi	*4-15*	*(14-28)*
Potentilla anserina Pl	*0-15*	*(0-32)*
Juncus inflexus LP	*11-15*	*(32-39)*
Centaurium pulchellum IN(LP)	*0-15*	*(0-40)*

d) species inundated during more than 16 weeks in the growing season and more than 32 weeks during a whole year. For species with an upper distribution limit the number of weeks is indicated.

Carex hirta LP		
Epilobium parviflorum Ph		
Oenanthe aquatica Ph	*11-18*	*(32->42)*
Samolus valerandi		
Juncus gerardi As		
Drepanocladus aduncus		
Alisma plantago-aquatica Ph		
Mentha aquatica Ph	*11-19*	*(32->42)*

Ranunculus sardous LP
Eleocharis uniglumis LP
Ranunculus sceleratus Bi
Rorippa islandica Bi
Rumex maritimus Bi
Juncus articulatus
Bidens cernua Bi 7-21 (28-41)
Glyceria declinata
Ranunculus repens
Poa trivialis MA
Nasturtium microphyllum Ph
Eleocharis palustris Ph
Alopecurus geniculatus LP
Agrostis stolonifera LP
Glaux maritima As
Scirpus maritimus Ph
Plantago major Pl
Juncus bufonius IN
Phragmites australis Ph
Scirpus lacustris Ph
Veronica catenata Bi 2-26 (15->42)

4. Discussion

Varying hydrological conditions lead to zonations of different degrees of clarity. On sandy well-drained soils the zonation is clear. On sandy to clayey loam soils with a higher water retention capacity or on soils where drainage is impeded, for example by a peat layer, the soil of even the highest quadrats may be waterlogged during the greater part of the year. Under these conditions the zonation is diffuse and the vegetation change is more gradual. On sandy well-drained soils three zones can be distinguished:

1) a zone which is never inundated;
2) a middle zone below the highest water level in winter;
3) the lower zone which is inundated almost continuously or which has a soft, severely poached, waterlogged soil. When a contrasting difference exists between the inundation length of the upper and the lower

quadrats of the middle zone two subzones may form. In the case of a diffuse zonation the non-flooded and the flooded zone gradually shade off into one another.

The *Lolio-Potentillion* alliance has its optimum between the never inundated sites and the sites which are inundated during the greater part of the year. This habitat is characterized by a strongly changing water regime. Under conditions of impeded drainage the *Lolio-Potentillion* species also occur at sites which are never inundated. Under these conditions as shown by the transects Koegat and Cambron in this study, the flooding is replaced by prolonged waterlogging of the soil, both impacts resulting in oxygen depletion in the rhizosphere (ERNST 1979).

In this study *Elymus repens* occurred exclusively on non-inundated sites. This is in accordance with its syntaxonomic position; it is a differential species of the *Ranunculo-Alopecuretum geniculati* subassociation *rorippetosum sylvestris* (SÝKORA 1982a). This subassociation is confined to sites with a low ground water table and a dry top soil after the retreat of the water. Some *Lolio-Potentillion* species occurred on sites inundated for certain periods in both the summer and the winter season viz. *Trifolium fragiferum*, *Carex otrubae*, *Potentilla anserina* and *Juncus inflexus* (see section 3.4.c) . *Trifolium fragiferum*, the character-species of the *Agrostio-Trifolietum fragiferi*, is recorded to tolerate up to 8 weeks of inundation during the summer season and up to 29 weeks during a whole year. A number of other character- and differential species of the alliance even occurred on sites inundated during more than 16 weeks in the growing season and more than 32 weeks in a whole year, viz. *Carex hirta*, *Ranunculus sardous*, *Eleocharis uniglumis*, *Alopecurus geniculatus*, *Agrostis stolonifera* and the species differential for the *Nasturtio-Alopecuretum geniculati*, viz.*Nasturtium microphyllum*, *Ranunculus sceleratus*, *Veronica catenata* and *Epilobium parviflorum* (see section 3.4.d).

The *Nasturtio-Alopecuretum* occurs on very soft, severely poached soils which are waterlogged throughout the year. Apart from these species, the species occurring on sites inundated during more than 16 weeks in the growing season mainly belong to the *Bidention* and the *Phragmitetea*.

The *Molinio-Arrhenatheretea* species are mainly restricted to sites

which are not flooded during the growing season. Only *Holcus lanatus*, *Taraxacum officinale* group, *Bellis perennis* and *Leontodon autumnalis* have been recorded to tolerate inundation during this period.

Yearly changes in the hydrological situation lead to fluctuations in the vegetation. Many species increased in 1980, the year with summer inundation in July, and subsequently decreased in 1981. This corresponds with the findings of BALATOVÁ-TULÁCKOVÁ 1962. In the non-flooded zone these species belong to the *Molinio-Arrhenatheretea* which are sensitive to inundation and to the *Lolio-Potentillion*, *Bidention* and *Phragmitetea*, which are tolerant of inundation. *Festuca rubra*, *Juncus gerardi* and *Ranunculus repens* decreased in 1980 and increased in 1981. *Festuca rubra* has experimentally been shown to die under waterlogging conditions (JONES & ETHERINGTON 1971); it is uncertain however, whether the ecotype used by them (taken from a calcareous dune slack in Glamorganshire) corresponds in its ecological behaviour to the ecotype studied by us, which may be assigned to *Festuca rubra* ssp.*littoralis* C.A. Web.

Cynosurus cristatus (Lolio-Cynosuretum), *Carex otrubae*, *Eleocharis uniglumis (Lolio-Potentillion)* and *Juncus bufonius* decreased both in 1980 and in 1981. In the middle zone the species which increased in 1980 and decreased in 1981 mainly are those typical of the *Lolio-Potentillion*, the *Plantaginetea* and the *Phragmitetea*. *Centaurium pulchellum (Isoeto-Nanojuncetea)*, *Leontodon autumnalis (Arrhenatherion)* and *Lotus tenuis (Armerion)* also showed this fluctuation. Besides *Carex distans*, *Glaux maritima (Asteretea tripolii)*, *Eleocharis uniglumis*, *Ranunculus sardous (Lolio-Potentillion)*, *Scirpus lacustris* ssp.*tabernaemontani*, *Glyceria fluitans (Phragmitetea)*, *Lolium perenne* and *Plantago major (Plantaginetea)* increased in 1980.
The *Molinio-Arrhenatheretea* species *Festuca rubra* and *Poa trivialis* and the *Lolio-Potentillion* species *Eleocharis uniglumis* increased in 1981.

Fluctuations in the lower zone were mainly shown by the *Bidention* species, annual species of bare, wet and nutrient-rich mud (VAN DER TOORN 1980) and also by some *Lolio-Potentillion* and *Phragmitetea* species which increased in 1980 and decreased in 1981. *Ranunculus baudotii (Callitricho-Batrachion)* has only been observed in 1980. *Eleocharis uniglumis (Lolio-Potentillion)*, *Juncus bufonius (Isoeto-Nanojuncetea)*,

Juncus gerardi (Asteretea) and *Scirpus lacustris* ssp.*tabernaemontani (Phragmitetea)* increased in the year with summer inundation (1980). In 1981 *Alopecurus geniculatus* and *Carex hirta (Lolio-Potentillion)*, *Potentilla anserina (Plantaginetea)*, *Phragmites australis (Phragmitetea)* and *Trifolium repens (Arrhenatherion)* decreased in the lower zone. Some *Phragmitetea* species *(Alisma plantago-aquatica, Eleocharis palustris, Epilobium parviflorum)* decreased after the summer inundation in 1980 and increased in 1981. The same behaviour was shown by *Lolium perenne (Plantaginetea).Phragmites australis*, *Scirpus maritimus (Phragmitetea)*, *Juncus inflexus (Lolio-Potentillion)*, *Potentilla anserina (Plantaginetea)* and *Glaux maritima (Asteretea tripolii)* decreased in this zone in 1980. The *Molinio-Arrhenatheretea* species *Poa pratensis* and *Poa trivialis*, the *Bidention* species *Chenopodium rubrum*, the *Phragmitetea* species *Oenanthe aquatica* and the *Lolio-Potentillion* species *Trifolium fragiferum* increased in 1981.

The fluctuation is not restricted to inundation-tolerant species. In the upper zone species of the *Molinio-Arrhenatheretea* which are sensitive to flooding also increased in the summer of 1980. This is in accordance with the statement of DE VRIES & KOOPMANS(1949) that wet years are the best grass years for the farmer. The high precipitation in July enhanced the growth of several species in the upper non-flooded zone of the transects. In the lower zones the *Lolio-Potentillion*, *Phragmitetea* and *Bidention* species occurring on regularly flooded soils are clearly stimulated by the summer inundation, the *Lolio-Potentillion* species especially in the middle zones. The stimulation of flood-associations by an increase of the flooding period and the reduction of species which cannot survive prolonged inundation periods has also been noticed by HUNDT 1975, BALATOVÁ-TULÁCKOVÁ 1972, KOPECKÝ 1967. STOFFERS & KNAPP (1962) demonstrated that after experimental flooding (33 days) of the inundation-tolerant *Agrostis stolonifera* grassland, the species composition did not considerably change; the biomass production however increased with lengthening period of flooding. However in the *Arrhenatheretum* after a period of five months almost all species were negatively influenced when inundated during 10.5 days. The expansion or contraction of the vegetation zones (VAN LEEUWEN 1958, see also Introduction) is only slight. The syntaxonomic position of the

vegetation occurring in the different zones did not change; no alternation of associations took place.

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PUBLICATION VII

A SYNECOLOGICAL STUDY OF THE LOLIO-POTENTILLION ANSERINAE R.TÜXEN 1947 BY MEANS OF PERMANENT TRANSECTS II: RIVERINE EURYSALEUTIC HABITATS.

Karel Vaclav Sýkora, Botanisch Laboratorium, afdeling Geobotanie, Katholieke Universiteit, Nijmegen.

Summary

The long term dynamics in the *Ranunculo-Alopecuretum geniculati* and adjacent vegetation has been studied by means of five permanent transects during four consecutive years, from 1978 to 1981. A correlation was found between the distribution of the species and both the length of the inundation period and the nutrient status of the soil. Oscillations in the hydrology resulted in ecotopic fluctuations of mainly the species characteristic of the *Arrhenatheretalia*, the *Bidentetalia*, the *Chenopodietea*, the *Nanocyperion* and the *Plantaginetea*. These species increased in years with short inundation periods and decreased in years with prolonged floodings during the growing season. Although ecotopic fluctuation could be rocorded for some of the *Lolio-Potentillion* species, viz. *Mentha pulegium*, *Alopecurus geniculatus*, *Trifolium fragiferum* and *Juncus compressus*, most of the species characterizing this alliance showed no correlation with fluctuations in the hydrology during the research period. In the eurysaleutic habitat the detection of zonation by means of single linkage clustering proved to be impossible.

1. Introduction

The present paper is the second of two sequential contributions dealing with the results of a synecological study of the *Lolio-Potentillion anserinae* by means of permanent transects. For floristic and ecological reasons this alliance has been separated from the *Agropyro-Rumicion crispi* Nordhagen 1940 em.R.Tüxen (SYKORA 1980). The *Lolio-Potentillion* (Class *Plantaginetea majoris*, Order *Agrostietalia stoloniferae* Oberdorfer, Müller & Görs 1967) is characterized by the character-species *Agrostis stolonifera*, *Rumex crispus*, *Alopecurus geniculatus* and the constant companion *Poa trivialis*. Apart from these the character-species

of the *Plantaginetea* TÜxen & Preising 1950, *Potentilla anserina*, *Plantago major*, *Lolium perenne* and *Poa annua* are present with often high presence degrees in most or in some of its communities.
The first paper about the permanent transects (SYKORA 1983) discussed the correlation between the zonation in the vegetation and the fluctuation of the species over the years on the one side and the hydrological dynamics in the brackish stenosaleutic habitats on the other. Stenosaleutic habitats are understood as brackish habitats in which the difference between the maximum and minimum water levels does not exceed 60 cm. The present paper deals with the permanent transects laid in fresh eurysaleutic riverine habitats. Here the hydrological dynamics are very pronounced, the difference between maximum and minimum water levels is considerably exceeding 80-100 cm and in most cases even surpassing five meters. The concepts "stenosaleutic" and "eurysaleutic" used have been derived from the classification of vegetation habitats on the banks of Czechoslovak water courses, as proposed by KOPECKY (1969).

Communities belonging to the *Lolio-Potentillion anserinae* R.TÜxen 1947 are mainly composed of reptant hemicryptophytes and rhizome-geophytes and occur in pastures on all kinds of relatively nutrient-rich, hydromorphic soils, inundated during winter and spring (SYKORA 1980, 1982a, b and c). The aim of the present paper is to describe:
1) the response of the species to the yearly fluctuations in hydrology i.e. the period of flooding;
2) the distribution of the species in relation to the period of flooding. To this aim the occurrence of ecotopic fluctuations (RABOTNOV 1974) i.e. fluctuations caused by changes in the ecotope, in this case the hydrological differences from year to year, has been examined (see also SYKORA 1983).

2. Methods

2.1. Physical set up of the transects

In 1978 five transects were established along the river Waal near Nijmegen (province Gelderland, the Netherlands), which river is the

main branch of the river Rhine.(see fig.1).

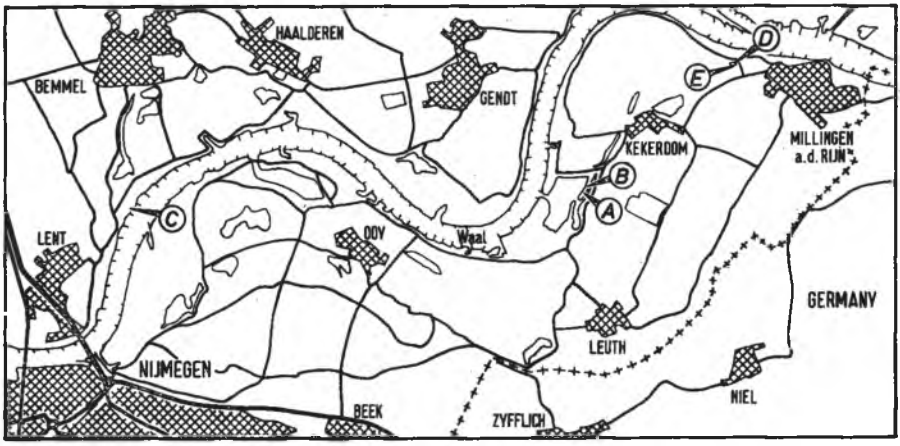


fig.1 Map of the study area near Nijmegen. The location of the transects A-E is indicated.

Three of the transects occur in the river forelands, one of them immediately on the bank of the river (transect C), the other two (transects A and B) on the bank of a former river bed now in connection with the present river through a narrow inlet. The remaining two transects (D and E) are situated on the bank of the Molenkolk, a pool resulting from a former dike burst, now occurring on the landside of the dike and consequently without direct contact with the river.

The transects were made on slopes perpendicular to the waterline, each forming a transverse section through a previously selected stand of *Lolio-Potentillion* vegetation and adjoining communities. The length of the transects A, B, C, D and E is respectively 30, 22, 56, 13 and 37 metres. The level of the quadrats is given at the top of the tables 2-6 (see appendix). The variation in length of the transects depends on the inclination of the slope. On steeper slopes the zonation is telescoped. Unfortunately in 1979 the transects A and B were dug down by the local brick-works. Although transect A disappeared totally, the sampling of the last 14 quadrats of transect B could be continued.

2.2. Analytical research phase

The transects were sampled by means of contiguous quadrats sized 2 x 1 m (transect A, E and the quadrats 1-18 in the case of B), 2 x 0.5 m (D and quadrats 19-26 of B) and 2 x 4 m (C). The size of the quadrats has been chosen in relation to the steepness of the slope. All quadrats were placed with their long side at right angles to the transect line. Sampling took place during four consecutive years from 1978 to 1981, in several cases twice a year.
The quantitative occurrence of each species was estimated using the Braun-Blanquet scale as refined by BARKMAN et al (1964, see also WESTHOFF & VAN DER MAAREL 1973).

Data on the free water level of the river Waal (fig.2-4) were taken from the monthly reports as given by the Department for the Maintenance of Dikes, Roads, Bridges and the Navigability of Canals (Rijkswaterstaat). The free water level of the Molenkolk as well as the soil water table nearby transects D and E were measured by H.M. van de Steeg (fig.5).
Soil samples were collected from April-October at intervals of four weeks in three (transect B) respectively four (transects C and D) sampling sites at both sides of each transect which gives a total of six respectively eight sampling sites / transect. Each sample was composed of a mixture of five subsamples. Location of the sampling sites was for transect B at both sides of the quadrats 13, 18 and 26, for transect C of the quadrats 1, 14, 22 and 28 and for transect D at both sides of the quadrats 1, 9, 18 and 26. As the majority of the roots were concentrated in the top 5 or 10 cms, all samples were collected from depths of 1-6 cm. After extraction with bidest the samples were analysed for PO_4^{3-}, NH_4^+, NO_3^- and NO_2^-, using a Technicon autoanalyser. Furthermore organic content, soil texture, pH, total N and P, $CaCO_3$ and pore volumes were determined once only. The destruction of the samples used for analysing total N, was according to WALKLEY & BLACK (1934). Total N content was measured colorimetrically after Kjeldahl-destillation. H_2SO_4 and H_2O_2 were used for the destruction of the samples in case of the analysis for total P content. Total P content was measured colorimetrically as well. The $CaCO_3$ content was analysed according

to SCHEIBLER & FINKENER.
Pore volumes of 100 cc soil samples were measured by means of a vacuum air pycnometer according to LANGER.

2.3. Synthetical phase

The species were positioned in tables (tables 2-6, see appendix) in such a way that their distribution along the transects is clearly shown. By means of single linkage clustering using the similarity ratio (WISHART 1978) the possible presence of boundaries was examined. As the quadrats were chained and no clear clustering occurred in the dendrograms thus constructed, no indication of boundaries could be found. In order to reduce the number of figures these diagrams have been omitted from the present paper.

Reciprocal averaging (HILL 1973) of all the plots sampled in all years has been used for species ordination. As the rationale of the method is close to that of gradient analysis, it is more suitable than principal components analysis for displaying strong floristic gradients.

For each species the total range in respect to the duration of inundation in weeks during the growing season has been determined. The range of a species is defined as the region between its highest and its lowest position in a transect within one given year. Thus a species occurring in two transects in three years gives six ranges.
A relative value for the quantitative occurrence of the species in relation to the duration of the flooding taking into account the ranges in the separate years and transects is indicated in fig. 7b. This value (R) has been calculated by determining the average number of weeks (x) during which each species was flooded in any transect and any year, adding these values and dividing them by the number of observations (ranges). This can be expressed as:

$$x_1 = \frac{hp + lp}{2}$$

in which hp = the inundation period at the highest position of range 1;
lp = idem at the lowest position of range 1.

$$R_A = \frac{x_{1 \rightarrow n}}{n}$$

in which n= the number of the ranges for species A;
R_A = relative value for species A.

If the range of a species continues above or beneath the limits of a transect, the inundation period registered at one of the extremes of the transect had to be used in the calculations. In order to calculate the decrease or increase of the species the sum of the transformed cover-abundance values of every species in each part of the table was compared from year to year (tables 7-11).

In all numerical methods used above the extended scale of BARKMAN et al. (1964) was transformed into a 1-9 numerical scale according to the ordinal transformation (VAN DER MAAREL 1979).

Species nomenclature follows the Flora Europaea (TUTIN et al. 1964-1980) for phanerogams and LANDWEHR (1966) for bryophytes.

3. Results and discussion

3.1. The transects

3.1.1. Abiotic environment

Hydrology (figs. 2-5).

The hydrology of the sites is very dynamic. Inundations occur both in winter and summer. The frequency of flooding as well as the period and depth of flooding are unpredictable. The difference between maximum and minimum water level is considerable and at times exceeds five metres. All transects are totally flooded during periods of high water. From all transects, transect C, being in direct contact with the river, is most exposed to the current. In the lower quadrats of this transect signs of sedimentation and erosion are obvious. Transect D and E are influenced only indirectly by the river i.e. the free water of the pool is in contact with the river through the subsoil water beneath the dike. During high water periods water is percolating underneath the dike into the pool. The fluctuations in its water level is retarded in comparison

to that of the river (fig.4).

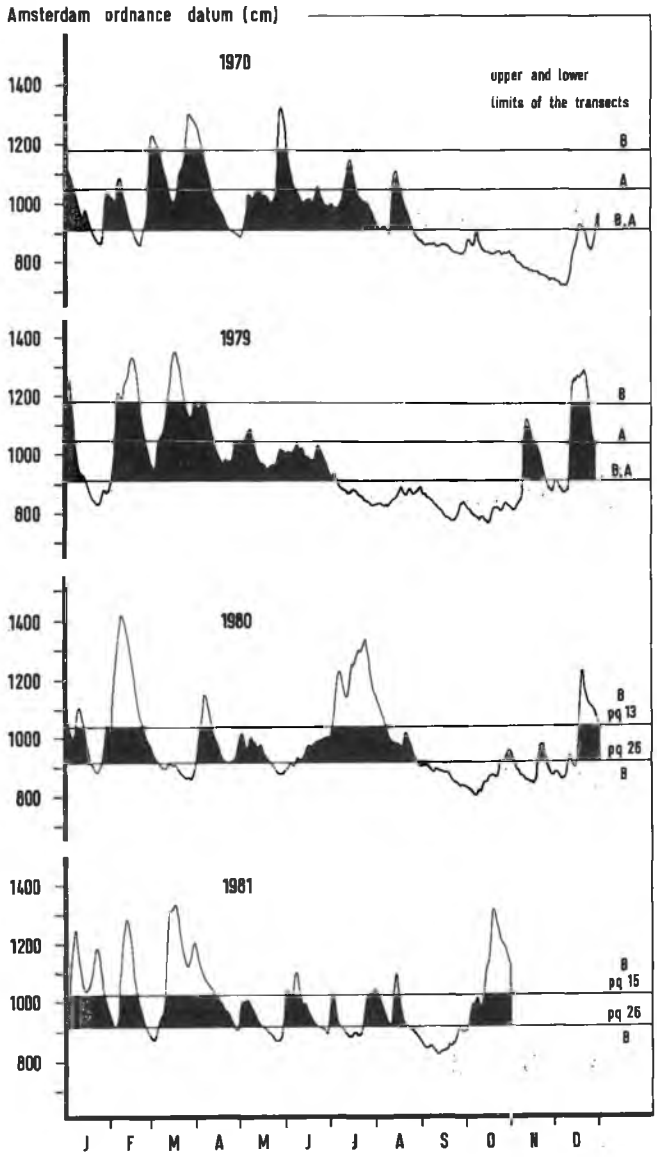


fig.2 Periods and depths of flooding in the transects A and B. The highest and lowest levels for every transect are indicated by horizontal lines. Transect A and the first 12 quadrats of transect B were studied in 1978 and 1979 only.

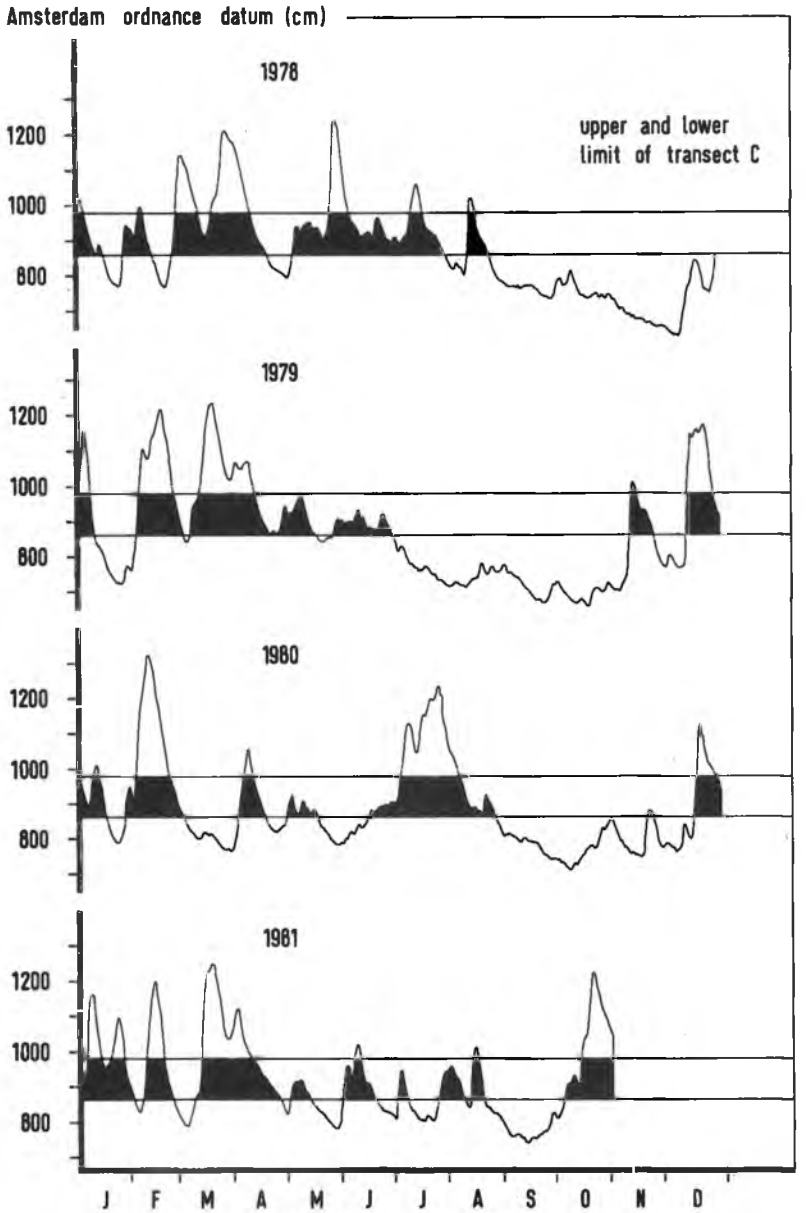


fig.3 Periods and depths of flooding in transect C. The highest and lowest levels for the transect are indicated by horizontal lines.

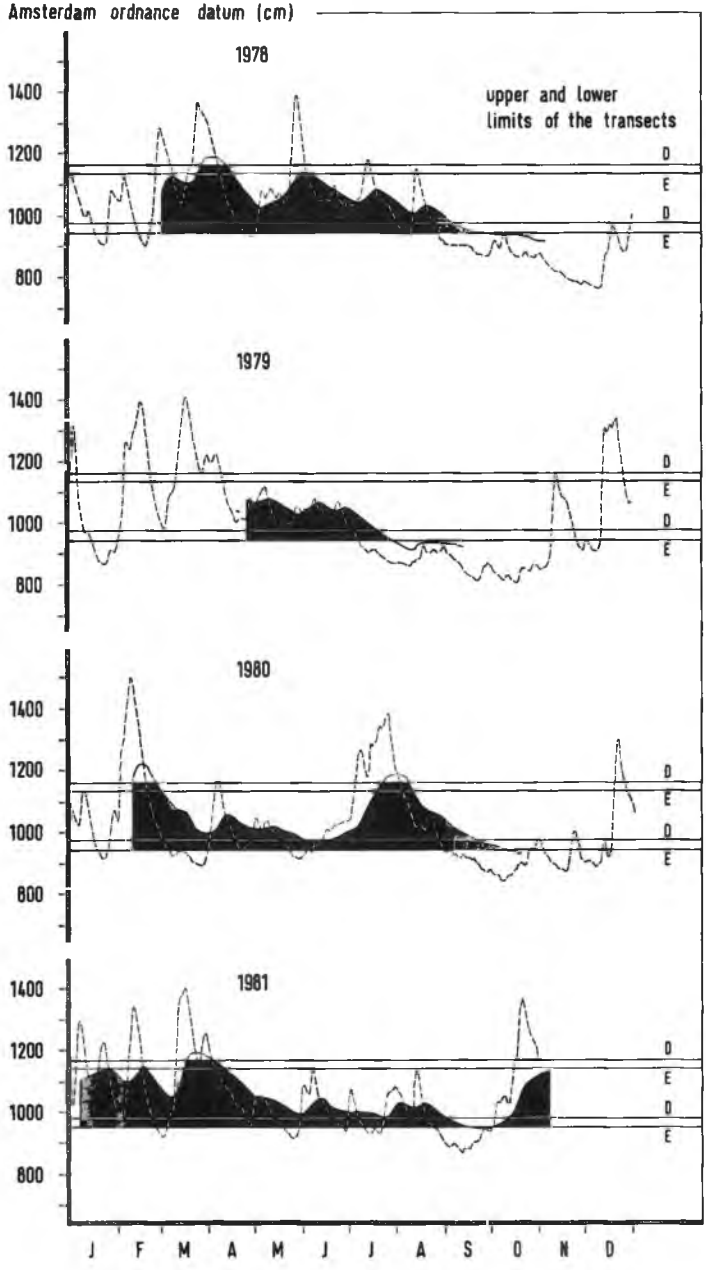


fig.4 Periods and depths of flooding in the transects D and E. The highest and lowest level for every transect are indicated by horizontal lines. For the water level of the river Waal see the interrupted line.

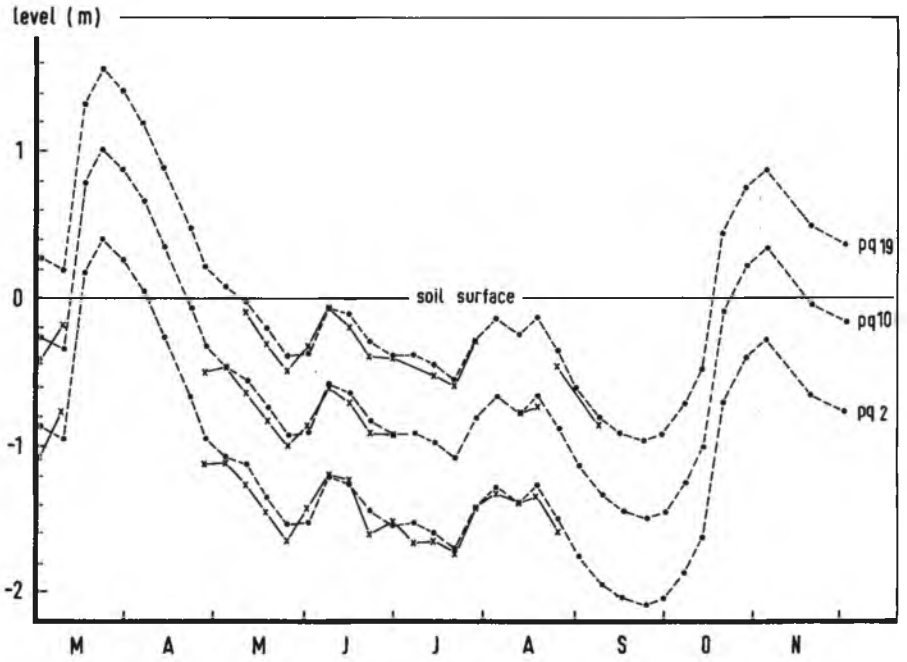


fig.5 The variation in the ground water level in the year 1981 (duration curves) in the quadrats 2, 10 and 19 from transect D (uninterrupted line). The water level of the pool is indicated by the interrupted line.

Consequently the hydrological dynamics are lower when compared to those in transect C. The transects A and B take an intermediate position as they are located at some distance from the river on the bank of a former river bed which is in contact with the present river through a narrow inlet only.

The ground water level measured in transect D corresponds with the free water level in the pool. In 1981 the deepest ground water levels for the quadrats 2, 10 and 19 were respectively -210, -150 and -97 cm (fig.5). This explains the occurrence of the subassociation *rorippetosum sylvestris (Ranunculo-Alopecuretum geniculati)* in this transect. This subassociation is confined to sites with a low ground water table

and a dry top soil after the retreat of the water (SYKORA 1982 a)
No ground water levels have been measured in the other transects.

Soil texture and organic matter content (see MILLAR et al. 1958).

Transect A: quadrat 1: sandy clay loam, other quadrats clay to silty clay;
organic matter quadrat 1: 7%, other quadrats 10-17%.
Transect B: sandy loam to loam; organic matter 3-13%.
Transect C: heterogeneous; clay loam, alternating with sandy loam (most of the quadrats) and sandy clay loam. The lowest quadrats vary from loamy sand to sand; organic matter 6-14%.
Transect D: loamy sand to sandy loam;organic matter 4-9%.
Transect E: loamy sand; organic matter 5-10%.

Pore volumes

The pore volumes are given in table 1. The highest volumes occur in the upper quadrats of transects D and C,the lowest volumes in transect B and in the lower quadrats of transects C and D.No measurements are available from transects A and E. Even the lowest volumes measured are not lower than the values found in a *Lolio-Cynosuretum* (45%) by BOEKER (1957). The air-filled pore volumes of the lower quadrats are very low however, even after emergence of these quadrats. This factor is probably considerably more important for the differentiation in the vegetation than the total pore volume as such.

Table 1. Total pore volumes and air-filled pore volumes determined in the permanent quadrats indicated. SD = standard deviation, n = number of samples.

location		pore volumes(%) total			pore volumes(%) air-filled 2 July 1979			pore volumes(%) air-filled 19 September 1979		
		$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
	p.q.1	56	3	6	43	0.6	3	38	3	3
D	p.q.9	59	5	6	15	4	3	34	5	3
	p.q.18	49	5	6	7	3	3	19	0.6	3

(Table 1 continued)

location		pore volumes(%) total			pore volumes(%) air-filled 2 July 1979			pore volumes(%) air-filled 19 September 1979		
		$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n
	p.q.1	49		1	37		1			
B	p.q.18	48	3	6	6	3	3	4	1	3
	p.q.1	68	3	6	35	3	3	22	3	3
C	p.q.14	61	7	6	10	6	3	25	2	3
	p.q.22	47	5	6	9	4	3	19	2	3

Total available N and P, PO_4^{3-}, NH_4^+, NO_2^- and NO_3^-

Total available P (mg/100 gr. dry sample) values are lowest for the transects D and E which are only indirectly in contact with the river Waal and highest for transects A and C. Transect B takes an intermediate position. Mean P values, standard deviations and number of observations are:

Transect A: $\bar{X}$= 186, SD= 31, n= 15.
Transect C: $\bar{X}$= 229, SD= 42, n= 16.
Transect B: $\bar{X}$= 105, SD= 45, n= 4.
Transect D: $\bar{X}$= 53, SD= 10, n= 4.
TRansect E: $\bar{X}$= 39, SD= 7, n= 4.

The pattern for total N values (mg/100 gr dry sample) is different. Transects A and E have higher mean values than transects B, C and D. Values for total N are:

Transect A: $\bar{X}$= 218, SD= 38, n= 16.
Transect E: $\bar{X}$= 272, SD= 86, n= 4.
Transect B: $\bar{X}$= 99, SD= 48, n= 4.
Transect C: $\bar{X}$= 103, SD= 53, n= 15.
Transect D: $\bar{X}$= 109, SD= 42, n= 4.

NH_4, NO_2^- and NO_3^- values show considerable temporal and spatial variability resulting in very high standard deviations; in several cases the standard deviations are even considerably higher than the mean

values. Consequently no conclusions can be drawn about any difference between the transects. Mean phosphate values, however, although still having high standard deviations, show the same trend as total P values. In B, C and D, the only transects where PO_4^{3-} has been measured, mean values are respectively 20 (SD= 12, n=18), 39 (SD= 21,n=32) and 11 (SD= 8, n=39).

C/N ratio

The C/N ratios indicate a fairly rapid mineralisation. In the transects in which it has been measured, the mean values are 15 (transect B, SD= 2), 14 (transect D, SD= 3) and 10 (transect E, SD= 2).

3.1.2. The vegetation

For the names of the syntaxa I refer to WESTHOFF & DEN HELD (1969) and to SYKORA (1982). Transects A and B form a transverse section through the *Ranunculo-Alopecuretum geniculati* subassociation *rorippetosum sylvestris* Sýkora 1982.In the upper part there is an element of the *Artemisietea* represented by *Urtica dioica*, *Rumex obtusifolius*, *Rumex* x *acutus* and *Glechoma hederacea*. The lower quadrats are without vegetation cover immediately following the retreat of the water. After approximately two weeks these quadrats are covered with representatives of the *Eleocharitetum soloniensis (Nanocyperion)* viz. *Juncus bufonius*, *Filaginella uliginosa*, *Limosella aquatica*, *Potentilla supina and Riccia crystallina*. In this part of the transect the *Bidentetalia* element is represented by *Bidens tripartita*, *Ranunculus sceleratus*, *Chenopodium rubrum*, *Chenopodium glaucum*, *Polygonum hydropiper*, *Atriplex hastata* and *Myosoton aquaticum*, the *Chenopodietea* element by *Stellaria media*, *Sonchus arvensis*, *Capsella bursa-pastoris* and *Matricaria perforata*.

In transect C, stands in which *Phalaris arundinacea* is dominant (the sociation of *Phalaris arundinacea (Magnocaricion)*) are alternating with patches of the *Ranunculo-Alopecuretum geniculati* subass. *rorippetosum sylvestris*. In the lower quadrats species from the *Bidentetalia* occur, viz. *Bidens tripartita*, *Chenopodium glaucum*, *Myosoton aquaticum*, *Chenopodium rubrum*, *Ranunculus sceleratus* and *Atriplex hastata*, the *Chenopodietea* viz. *Matricaria perforata*, *Conyza canadensis*, *Chenopodium poly-*

spermum and *Senecio vulgaris*, the *Artemisietea* viz. *Artemisia vulgaris*, *Cirsium arvense* and *Tanacetum vulgare*, and the *Nanocyperion* viz. *Potentilla supina* and *Filaginella uliginosa*. Most of these species are therophytes and are especially abundant in years without prolonged flooding in the growing season.

In transects D and E the vegetation presents a transition from the top downward from a *Lolio-Cynosuretum* into a *Ranunculo-Alopecuretum geniculati* subass . *rorippetosum sylvestris*. The lowest quadrats are poor in species. *Mentha pulegium*, a *Lolio-Potentillion* species which is very rare in the Netherlands, occurs in these transects. The species showed a considerable decline during the last century. Before 1950 it was recorded in 47 5-km squares, since 1950 the species has been found in 8 5-km squares (ADEMA 1980, 1981). The decline probably is due to the local changes in water control which in general led to drier soil conditions during the growth season. My soil data show that total P values at the transects D and E, in which *Mentha pulegium* occurs, are considerably below those in the other transects which suggests that eutrophication, especially enrichment with phosphorus, might also be responsible.

3.2. Vegetation boundaries and vegetation zonation

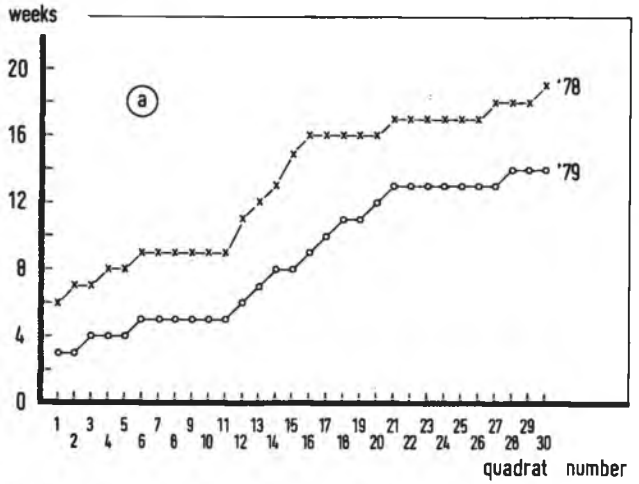
In the preceding paper (SYKORA 1983) about the brackish stenosaleutic habitats boundaries between different zones in the vegetation could be clearly detected by means of single linkage clustering. The presence and positions of these boundaries were explained by the hydrological characteristics. In the single linkage method the similarity between clusters P and Q is defined as the highest single similarity coefficient between two individuals, one from each cluster (WISHART 1978). Because of this characteristic the method is highly suitable for the detection of boundaries between contiguous quadrats in a transect. Nevertheless in the present study no zonation could be discovered in this way.

The absence of zonation in the transects most probably is due to the irregularity of the flooding. The frequency of flooding as well as the period and depth of flooding are unpredictable.

3.3. Ecotopic fluctuation (tables 7-11, see appendix).

As flooding during the growing season is of considerably more importance to the species than winter inundation (WALTHER 1977), ecotopic fluctuations as well as the species distribution have been related to the flooding period during that part of the year (1 April- 1 October). The damage is proportional a) to the sensitivity of the species for flooding, b) to the temperature of the water as its oxygen content is negatively temperature dependent , c) to the depth of the water and d) to the duration of the flooding. The damage is caused by oxygen depletion, mainly resulting from the high consumption of oxygen needed for the decomposition of the submerged organic material (KLAPP 1965, 1971, SÝKORA 1982, 1983). Plant activity and consequently the need for oxygen is stimulated by higher temperatures. According to KLAPP (1971) in a temperate climate growth of grassland species starts at 5° C. and abundant growth only above 10° C. As the water temperature of the river Waal usually reaches 10° C. in the beginning of April, this date was taken as the start of the growing season.

With the exception of some quadrats, the longest flooding in all transects occurred in the growth season of 1978 (fig.2-4, fig.6). After running dry in April, the transects were inundated once again in May and the river did not retreat until the end of July. In August the water level increased once more for a short period. Only after the end of August the transects emerged for some longer period. Consequently in 1978 the growth season was of a very short duration.
In 1979 the retreat of the water was more gradual (fig.2-4). The transects were not reflooded after the end of June resulting in a considerably shorter flooding period and a considerably longer growth season (fig.6).
In 1980 the flooding period lasted longer in almost all quadrats than in 1979 but shorter than in 1978. The transects were flooded during a short period at the beginning of April and the lowest quadrats again during the month of May. Subsequently all quadrats were inundated once more during a summer flood lasting from the beginning of June till the end of August. The fall of the water was irregular with varying rates at different periods of time.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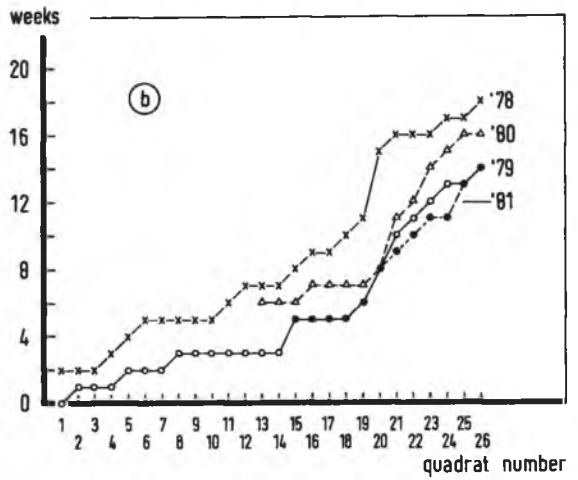
quadrat number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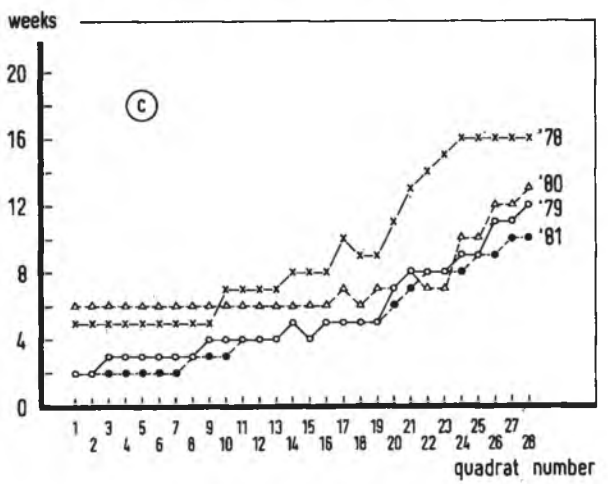
quadrat number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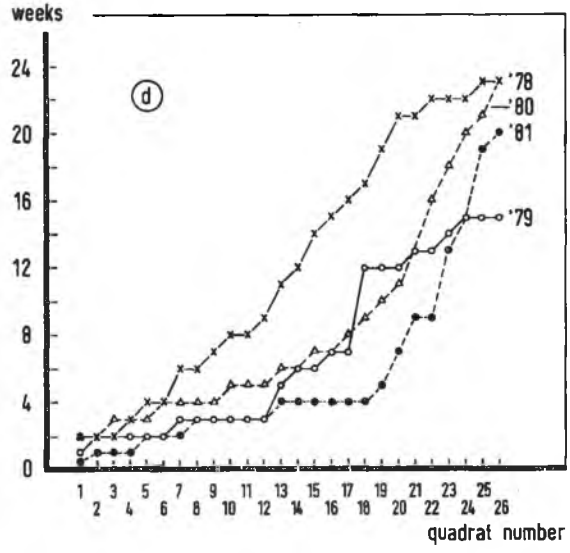
quadrat number



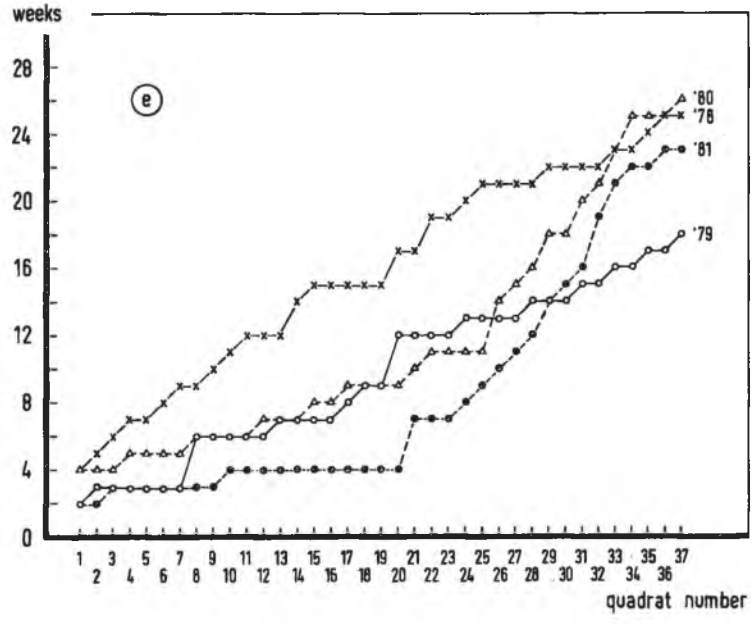


fig.6 Length of the period of submersion of the quadrats in the separate years. a = transect A, b = transect B, c = transect C, d = transect D and e = transect E.

In 1981 in almost all quadrats the period of inundation was shorter than in 1980. Many quadrats were flooded even shorter than in 1979 (fig.6). However flooding, though relatively short, was frequent and occurred in the first half of April, the first half of May, the first half of June, the first week of July and from the end of July till the middle of August immediately followed by a new inundation of short duration.

During the first days after their emergence the lower quadrats of transects A, B and C were without vegetation cover, but at the end of the growing season numerous therophytes and seedlings of other species grew in these quadrats (see appendix, tables 2-4). *Plantago major* (mainly ssp. *pleiosperma*), normally a rosette hemicryptophyte (DE LANGHE et al. 1978, MOLGAARD 1976), behaved as a therophyte under the hydrological conditions in the lower parts of the transects. Within one season the changes in the vegetation of the lower quadrats of transects D and E were less extreme.

Many species increased from the "wet" year 1978 into the "dry" year, 1979 viz.:

1. *Arrhenatheretalia*
   - *Bellis perennis*
   - *Dactylis glomerata*
   - *Hypochoeris radicata*
   - *Lysimachia nummularia*
   - *Plantago lanceolata*
   - *Ranunculus bulbosus*
   - *Trifolium dubium*
   - *Trifolium repens*
2. *Artemisietea*
   - *Artemisia vulgaris*
   - *Glechoma hederacea*
   - *Tanacetum vulgare*
   - *Urtica dioica*
3. *Bidentetalia*
   - *Atriplex hastata*
   - *Chenopodium glaucum*
   - *Chenopodium rubrum*
   - *Myosoton aquaticum*
4. *Chenopodietea*
   - *Chenopodium polyspermum*
   - *Conyza canadensis*
   - *Matricaria perforata*
   - *Polygonum persicaria*
5. *Nanocyperion (Eleocharitetum soloniensis)*
   - *Filaginella uliginosa*
   - *Limosella aquatica*
   - *Potentilla supina*
   - *Riccia crystallina*
6. *Plantaginetea*
   - *Plantago major*
   - *Poa annua*
   - *Sagina procumbens*
7. *Lolio-Potentillion*
   - *Mentha pulegium*
8. *Phragmitetea*
   - *Myosotis scorpioides*
   - *Oenanthe aquatica*
   - *Veronica beccabunga*

besides: *Ranunculus repens*

The *Arrhenatheretalia*-species occur on well- and moderately well drained soils and are sensitive to inundation. The *Bidentetalia*, *Chenopodietea* and *Nanocyperion* species are characteristic for open habitats.

The *Bidentetalia*- and *Nanocyperion*- species are summer annuals occurring on wet ground or on sites with a fluctuating watertable. The *Chenopodietea*- and the *Artemisietea*- species usually are ruderal and occur on disturbed sites. Most of the species mentioned show a pioneer character and can rapidly colonize open patches in the vegetation, in this case caused by long inundation. *Ranunculus repens* can quickly colonize open ground by the production of long stolons (HARPER 1957, STOFFERS & KNAPP 1962).These species may be classified as competitive ruderals sensu GRIME (1979).

In 1978 the growing period was too short for a full development of these species groups.A few species decreased from 1978 to 1979 viz. *Alopecurus pratensis*, *Juncus compressus*, *Poa trivialis* and *Rumex conglomeratus*.Hardly any change was shown by:

1) the *Lolio-Potentillion*- species *Carex hirta* and *Potentilla reptans*;
2) the *Arrhenatheretalia*- species *Festuca rubra* and *Leontodon autumnalis* and, besides, *Glyceria maxima*, *Phalaris arundinacea*, *Lolium perenne* and *Equisetum arvense*.

Almost all species which increased from the year with prolonged inundation 1978 to the "dry" year 1979, again decrease in the "wet" year 1980. The following species decreased in 1980:

1. *Arrhenatheretalia*
   Bellis perennis
   Dactylis glomerata
   Festuca rubra
   Hypochoeris radicata
   Plantago lanceolata
   Ranunculus bulbosus
   Taraxacum officinale
   Trifolium dubium
   Trifolium repens
2. *Artemisietea*
   Artemisia vulgaris
   Cirsium arvense
   Cirsium vulgare
   Tanacetum vulgare
   Urtica dioica
3. *Bidentetalia*
   Atriplex hastata
   Chenopodium glaucum
   Chenopodium rubrum
   Ranunculus sceleratus
4. *Chenopodietea*
   Chenopodium polyspermum
5. *Nanocyperion*
   Limosella aquatica
   Potentilla supina
6. *Plantaginetea*
   Lolium perenne
   Plantago major
   Poa annua
   Polygonum aviculare
7. *Lolio-Potentillion*
   Alopecurus geniculatus
   Mentha pulegium
8. *Phragmitetea*
   Oenanthe aquatica
   Veronica beccabunga
   Veronica catenata
9. *besides:*
   Mentha arvensis
   Ranunculus aquatilis
   Ranunculus repens

The long summer inundation of 1980 with the subsequent short growing season apparently prevented the full development of these species. This is in accordance with the data from RUNGE (1977) which indicate the impossibility of recolonisation of bare spots if the water level drops near the end of the growing season. It is noteworthy that even *Alopecurus geniculatus*, a very faithful character species of the *Lolio-Potentillion anserinae*, has been influenced negatively by the hydrological conditions in 1980.
A few species increased in 1980 viz.:

1. *Lolio-Potentillion*
   Juncus compressus
   Potentilla reptans
2. *besides*
   Galium palustre
   Geranium molle
   Polygonum hydropiper

Hardly any change was shown by:

1. *Lolio-Potentillion*
   Carex hirta
   Trifolium fragiferum
2. *besides*
   Leontodon autumnalis
   Polygonum persicaria

The period of inundation in 1981 was shorter than in 1980. Many of the species increasing in the "dry" year 1979 also increased in 1981. Contrary to the situation in 1979, the growing season of 1981 was regularly interrupted by short periods of flooding. This did not prevent the following species to increase in 1981:

1. *Arrhenatheretalia*
   Bellis perennis
   Lysimachia nummularia
   Plantago lanceolata
   Poa pratensis
   Taraxacum officinale
   Trifolium dubium
   Trifolium repens
2. *Artemisietea*
   Artemisia vulgaris
   Rumex obtusifolius
   Urtica dioica
3. *Bidentetalia*
   Polygonum mite
   Ranunculus sceleratus
4. *Chenopodietea*
   Geranium dissectum
   Matricaria perforata
   Polygonum persicaria
5. *Nanocyperion*
   Centaurium pulchellum
   Juncus bufonius
   Limosella aquatica
   Riccia crystallina

6. *Plantaginetea*
   Lolium perenne
   Plantago major
   Polygonum aviculare
7. *Lolio-Potentillion*
   Mentha pulegium
   Rumex crispus
   Trifolium fragiferum
8. *Phragmitetea*
   Rorippa amphibia
   Veronica catenata
9. besides:
   Geranium molle
   Juncus articulatus
   Leontodon taraxacoides
   Mentha arvensis
   Ranunculus repens

Only *Galium palustre* decreased; *Carex hirta* and *Leontodon autumnalis* did hardly change. With exception of the species mentioned above, most of the *Lolio-Potentillion* species did not show a uniform behaviour in the transects in the separate years and consequently no clear correlation was found with the fluctuation in the total duration of flooding. Only *Mentha pulegium* always decreased in "wet" years and increased in "dry" years. The populations of the geophytic *Carex hirta* proved to be very stable.

Agrostis stolonifera in 1979 increased in all transects except transect C. In 1980 the species remained equal in transects B and C, slightly increased in D and slightly decreased in transect E. In 1981 it slightly decreased in transects B and C and increased in D and E.

Alopecurus geniculatus proved to be able to increase quickly toward the end of the growing season. Nevertheless the total coverage of this species is highest in the years with shorter total duration of flooding and consequently the longest growing season.

Juncus compressus decreased in 1979 in all transects except in transect D in which it remained equal. It increased in 1980 and showed contrasting behaviour in the different transects in 1981. Probably its reaction on the length of the inundation is less clear in 1981 because in that year, although the total period of inundation was short, the separate submersions were spread over the entire growing season (figs.2-4). In general *Juncus compressus* is favoured by years with a long period of flooding in the growing season. In September the species quickly disappears above ground.

Potentilla reptans did not increase during the "dry" year 1979, but did so during the "wet" year 1980 and , like *Juncus compressus* it showed contrasting behaviour in 1981. This species increases towards the end of every growing season.

Trifolium fragiferum has only been found in transects D and E (Molenkolk). In transect D it clearly increased in the years with a shorter inundation period. In transect E the change was only slight. Considering all transects no correlation could be found between the changes in cover of *Rorippa sylvestris*, *Rumex crispus*, *Inula britannica* and *Elymus repens* and the length of flooding.

From *Inula britannica* only a few individuals occurred in the transects (transect B, table 3a, Transect C, table 4d, transect E,table 6 a,b and d). According to KNEEPKENS & VERHOEVEN (1975) it is susceptible to competition with grasses. The *Plantaginetea* species *Plantago major*, although usually hemicryptophytic, behaved as a therophyte in the lower quadrats. These quadrats (transects A, B and C) were also covered by numerous seedlings of *Rumex crispus*, a species which is known to behave as an annual in arable land (CAVERS & HARPER 1964). It can germinate in any month of the year as long as conditions are not too cold or too dry and it is able to establish quickly and flower in the first year. Adult individuals of *Plantago major* and *Rumex crispus* die in the lower quadrats following prolonged inundation during the growing season.

3.4. Species distribution in relation to the period of submersion and the nutrient status of the soil.

The configuration in figs. 7 results from an ordination of the species of all the relevés made during the total research period (1978-1981). In the legend of fig.7a the total range for each species as regards the period of submersion in weeks, is indicated after the species names. In fig.7b the species numbers have been substituted by the relative inundation values (see 2.3.) Species with a low relative inundation value occur in the upper part of the diagram and increase downward. This indicates that the second axis corresponds with the behaviour of the species in relation to the period of flooding. The *Lolio-Potentillion* species have wide amplitudes with respect to the inundation period. They occur from sites hardly or never inundated during the growing season to sites that can be inundated from 21 to 26 weeks during the growing season. Only *Trifolium fragiferum* , number 78 in fig.7a, a character-species of the *Agrostio-Trifolietum fragiferi* SYKORA 1982, was absent from sites

inundated during more than 15 weeks.

The *Lolio-Potentillion* species can be ordered according to the relative inundation value as follows (their total range is indicated in parentheses):

	eurysaleutic habitat	stenosaleutic habitat
Inula britannica (nr.70)	6(<2-17)	
Trifolium fragiferum (nr.78)	7(<2-15)	(0-8)
Elymus repens (diff. species, (nr.1)	7(0-22)	(0)
Rumex crispus (nr.9)	8(1-21)	
Alopecurus geniculatus (nr.21)	9(<2-23)	(0->21)
Potentilla reptans (nr.11)	9(0-23)	
Agrostis stolonifera (nr.7)	10(0-26)	(0->21)
Mentha pulegium (nr.73)	11(0-23)	
Carex hirta (nr.37)	11(0-24)	(0->16)
Rorippa sylvestris (nr.12)	11(1-25)	
Potentilla anserina (nr.18)	12(2-23)	(0-15)
(Plantaginetea)		
Juncus compressus (nr.53)	12(3->25)	

Poa annua (nr.71) and *Chenopodium glaucum* (nr. 61) appear to be plotted too high in relation to their relative value.It should be kept in mind however, that both species possess extraordinary wide ranges as regards the iundation period: they were found in hardly inundated quadrats as well as in quadrats flooded during a long period.

Centaurium pulchellum (nr. 81) and *Geranium molle* (nr. 82) are plotted too low. *Geranium molle* has only been recorded in transect E with low cover both in two upper quadrats in the "wet" year 1980 and in four lower quadrats of the "dry" year 1981. As the ordination is based on the whole species combination of the vegetation and as the species occurred in more quadrats having a species combination characteristic for the lower part of the transect, it is consequently plotted in the lower part of the diagram. *Centaurium pulchellum* has only been found once viz. in the "dry" year 1981, when even the lower quadrats were inundated during a relatively short time and the vegetation there remained characteristic for the sites with a longer flooding period.

In order to compare the above mentioned results with the moisture indicator values of vascular plants as given by ELLENBERG (1979) for

central Europe these values have been plotted in fig. 7c. The arrangement of the indicator values in the diagram corresponds largely with the arrangement of the relative inundation values. This again suggests the second axis to correspond to a hydrological factor. *Glyceria maxima*'s (nr.3) position in the upper part of the diagram is curious; although it is normally found on wet, frequently inundated soils, in the transects it has only been recorded from the upper part of transect A. *Cirsium vulgare* (nr.50), a species indicative for fresh soils, here is found in the lower part of the diagram, because only seedlings of this species have been recorded in lower quadrats, some time after the retreat of the water.

The nitrogen figure (i.e. the occurrence in relation to the ammonia or nitrate supply (fig.7d)) increases, with some exceptions, along the first axis from right to left suggesting that the first axis corresponds to the nutrient status of the soil. The species occurring exclusively or mainly in transects D and E at the Molenkolk and which are reached only indirectly by the water of the river Waal, are plotted on the right side of the diagram. The opposite applies for species with their main occurrence in the transects in the river forelands and which are regularly inundated by the eutrophicated water of the river. The species range from those most common on poor soils (right side) to species only occurring on soils indicating pollution. Because of the great number of quadrats their ordination plotting was impossible. The quadrats were clearly ranked however along the first axis beginning with quadrats from transects D and E, followed by B and ending with quadrats exclusively from transects A and C. The mean values of total phosphorus and phosphate contents measured were lowest in transects D and E, highest in A and C and intermediate in B. This again suggests the first axis to correspond to the nutrient status of the soil. As the measurements of total N showed a different pattern and as the data on NH_4^+, NO_2^- and NO_3^- values were not conclusive, phosphate is probably of more importance for the differentiation mentioned above. From all the indicator values given by ELLENBERG (1979) his nitrogen figures are based most on experience and least on well-founded experimental data. In many cases these figures will merely indicate the general nutrient status instead of the occurrence in relation to ammonia or nitrate supply.

In fig.7e of the ordination diagram the difference in nutrient status is reflected by the presence of *Arrhenatheretalia* species on the right side of the first axis and the presence of the species of the *Bidentetalia*, *Artemisietea*, *Chenopodietea* and *Eleocharitetum soloniensis* (Hayek) Moor 1936 at the left. The *Bidentetalia*, *Chenopodietea* and *Artemisietea* are all nitrophilous weed communities, the *Bidentetalia* from habitats subject to periodic inundation, the *Chenopodietea* from rootcrop fields and waste places; the *Artemisietea* comprise tall herb weed communities from roadside verges, banks of canals and rivers (WHITE & DOYLE 1982, WESTHOFF & DEN HELD 1969, SHIMWELL 1971, RUNGE 1980). The *Eleocharitetum soloniensis* occurs on open places in the river forelands. According to WALTHER (1977) this community is favoured by a high nutrient status, especially a high nitrogen content of the soil. The *Arrhenatheretalia* occur on soils which are less rich in nutrients. Species characteristic for this order and represented in the ordination diagram, range from nitrogen figures indicating poor soils to those indicating soils rich in mineral nitrogen. Most of the *Arrhenatheretalia* species in the ordination diagram are however indicative for intermediate soils.

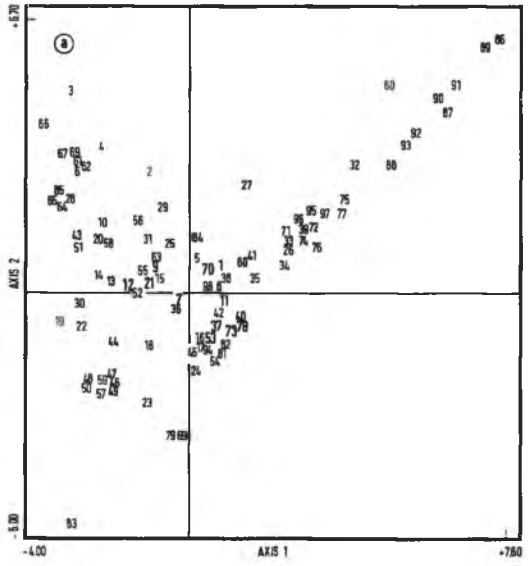


fig.7 Ordination (reciprocal averaging) of the species occurring in the transects in the years 1978-1981. a) species numbers. The inundation period during the growth season (in weeks) is indicated in parentheses:

(see next page)

1 Elymus repens (0-22), 2 Glechoma hederacea (0-9), 3 Glyceria maxima (<3-7), 4 Rumex obtusifolius (0-13), 5 Poa trivialis(0->19), 6 Urtica dioica(<2-17), 7 Agrostis stolonifera(0-26), 8 Ranunculus repens(0-19), 9 Rumex crispus(1-21), 10 Phalaris arundinacea(1-19), 11 Potentilla reptans(0-23), 12 Rorippa sylvestris(1-25), 13 Mentha arvensis(4-16), 14 Rorippa amphibia(<2-23), 15 Plantago major(0->19), 16 Myosotis scorpioides(0->25), 17 Veronica catenata(3-22), 18 Potentilla anserina(2-23), 19 Carex acuta(5-19), 20 Rumex x acutus(6-13), 21 Alopecurus geniculatus(<2-23), 22 Potentilla supina(2->14), 23 Polygonum amphibium(<2->26), 24 Eleocharis palustris(3->25), 25 Polygonum aviculare(3-17), 26 Bellis perennis(0-7), 27(Trifolium pratense(0-1), 28 Polygonum persicaria(0-11), 29 Rumex conglomeratus(3-7), 30 Veronica beccabunga(2-19), 31 Stellaria media(<2-18), 32 Cerastium fontanum(0-12), 33 Poa pratensis(0-17), 34 Trifolium repens(0-12), 35 Taraxacum officinale(0-15), 36 Equisetum arvense(0->18), 37 Carex hirta(0-24), 38 Cirsium arvense(0-21), 39 Plantago lanceolata(0-12), 40 Calliergonella cuspidata(<0.5->23), 41 Lysimachia nummularia(0-16), 42 Juncus articulatus(<2-22), 43 Atriplex hastata(<2->18), 44 Matricaria perforata(<2->26), 45 Juncus bufonius(2-21), 46 Ranunculus sceleratus(10->19), 47 Riccia crystallina(11->18), 48 Filaginella uliginosa(<7->19), 49 Oenanthe aquatica(11->19), 50 Cirsium vulgare(11->14), 51 Chenopodium rubrum(4->19), 52 Galium palustre(6-16), 53 Juncus compressus(3->25), 54 Mentha aquatica(4-16), 55 Polygonum mite (5-8), 56 Polygonum hydropiper(0->18), 57 Nymphoides peltata(14->16), 58 Bidens tripartita(<2->19), 59 Limosella aquatica(10->18), 60 Achillea millefolium(0-3), 61 Chenopodium glaucum(3-14), 62 Artemisia vulgaris (0->13), 63 Capsella bursa-pastoris(3-14), 64 Achillea ptarmica(3-5), 65 Helianthus annuus(4-6), 66 Galinsoga ciliata(<2-2), 67 Scrophularia auriculata(2), 68 Eupatorium cannabinum(2), 69 Drepanocladus aduncus (4-25), 70 Inula britannica(2-17), 71 Poa annua(0->23), 72 Lolium perenne(0-14), 73 Mentha pulegium(0-23), 74 Leontodon autumnalis(<1-11), 75 Cardamine pratensis(3-4)76Leontodon taraxacoides(1-3)77Trifolium dubium(0-7), 78 Trifolium fragiferum(<2-15), 79 Butomus umbellatus(5-24), 80 Geranium dissectum(<2-4), 81 Centaurium pulchellum(3-7), 82 Geranium molle(<4-9), 83 Lemna minor(17->19), 84 Alopecurus pratensis(0-5), 85 Brachythecium rutabulum(5), 86 Crepis capillaris(2), 87 Senecio jacobaea(3-4), 88 Deschampsia cespitosa(4), 89 Cynosurus cristatus(2), 90 Ranunculus bulbosus(0-3), 91 Festuca rubra(<1-4), 92 Dactylis glomerata(0-4), 93 Hippochoeris radicata(<1-7), 94 Ranunculus aquatilis(3-23), 95 Rumex acetosa(4-5), 96 Festuca pratensis(<2-7), 97 Convolvulus arvensis(<2-3), 98 Myosoton aquaticum(<5->14).

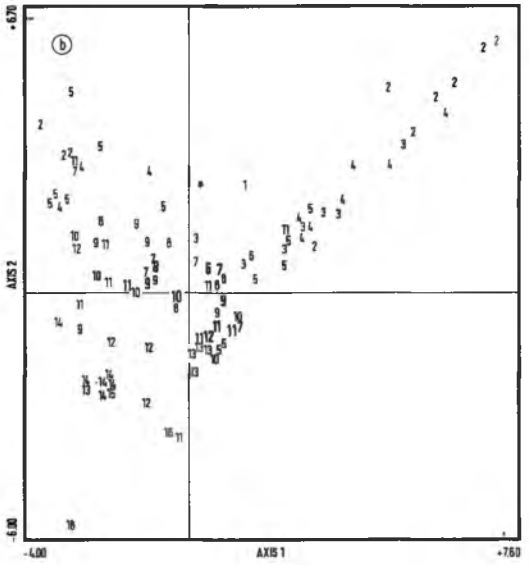


fig.7b Relative inundation values (see Methods, 2.3.).

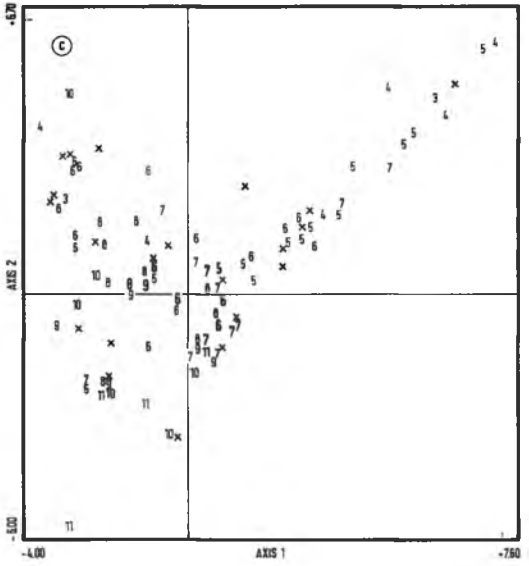


fig.7c Indicator values (ELLENBERG 1978), moisture figure i.e. occurrence in relation to soil moisture or water level.3=dry soils, 5=on fresh soils,i.e. under intermediate conditions, 7=on moist soils which do not dry out, 9=in wet,often not well aerated soils, 10=in frequently inundated soils, 11 =water plant whose leaves mostly are in contact with the open atmosphere.

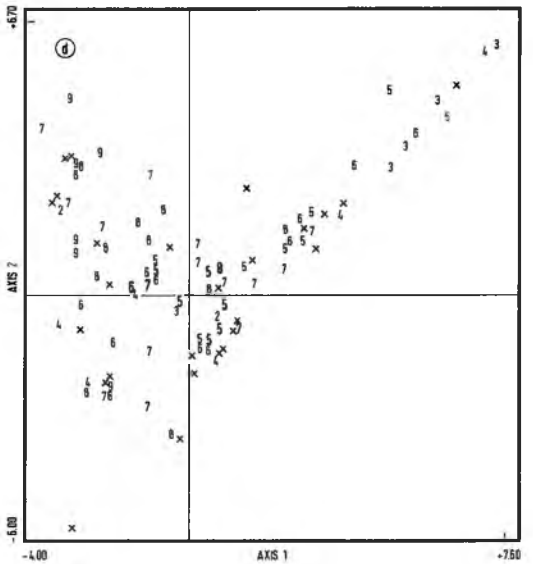


fig.7d Indicator figures (ELLENBERG 1978), nitrogen figure i.e. occurrence in relation to ammonia or nitrate supply. 3=mostly on poor soils, 5=mostly on intermediate soils, 7=mostly on soils rich in mineral nitrogen, 8=nitrogen indicator, 9=only on soils very rich in mineral nitrogen(indicating pollution,manure deposition or the like).

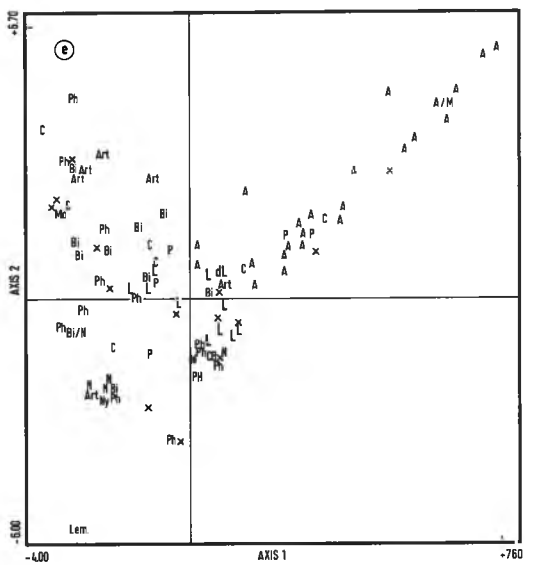


fig.7e Syntaxonomic status of the species. A=*Arrhenatheretalia*, M=*Mesobromion*, P= *Plantaginetea*, C= *Chenopodietea*, dL= differential species *Lolio-Potentillion*, L= *Lolio-Potentillion*, Mo= *Molinietalia*, Ph=*Phragmitetea*,N= *Nanocyperion*,Lem= *Lemnetea*,Ny= *Nymphaeion*,Bi= *Bidentetalia*,Art= *Artemisietea*, CB= *Callitricho-Batrachion*.

4. Conclusion

No zonation could be detected in the vegetation of the transects from the eurysaleutic habitat. This absence of zonation can be attributed to the irregularity of the flooding, i.e. the unpredictability of the frequency as well as the period and depth of the flooding. The species distributions are correlated with the length of the inundation period and with the nutrient status of the soils. Although the pore volumes are not lower than those found in the *Lolio-Cynosuretum*, the air-filled pore volumes of the lower quadrats are very low during a great part of the year. This apart from the length of the inundation itself must be very important for the distribution of the species.

The *Lolio-Potentillion* species have wide amplitudes with respect to the length of the inundation period and occur from sites hardly inundated or even without submersion during the growing season, to sites that have been recorded inundated from (17)21 to 26 weeks during the growing season. The optimum for these species is however nearer to the quadrats with the maximum values than to the uninundated quadrats. *Elymus repens*, a differential species of the subassociation *rorippetosum sylvestris (Ranunculo-Alopecuretum geniculati)*, a subassociation occurring on sites with a low ground water table after the retreat of the water, occurs predominantly on high marshes (SYKORA 1982 a, THOMAS et al.1981). This is in accordance with its low relative inundation value when compared to the other *Lolio-Potentillion* species. The species is very resistant to drought (DE VRIES 1948).

Fluctuations in the hydrology over the years studied resulted in ecotopic fluctuations in the vegetation (see also KOPECKY 1967, WALTHER 1977, ERNST 1979, HUNDT 1975). In years with a short period of inundation, mainly an increase of species characteristic for the *Arrhenatheretalia*, the *Bidentetalia*, the *Artemisietea*, the *Chenopodietea*, the *Nanocyperion* and the *Plantaginetea* can be observed. On the other hand, in years with long periods of flooding species characterizing these communities decrease again. Many of these species are therophytes and have a pioneer character. The decrease in wet years most probably is mainly due to the insufficient length of the remaining part of the growing season after the last inundation in that season.

For most of the *Lolio-Potentillion* species no clear correlation with the fluctuation in the hydrology could be shown. *Mentha pulegium* decreased in all "wet" years and increased in all "dry" years. The species belongs to the trichohygrophyta: this means that germination and development occur in the terrestrial phase. The above ground organs of plants belonging to this life form can withstand inundation with relatively warm water only shortly. If the temperature of the water is low, it can live through the unfavourable period viz. winter and spring (HEJNÝ 1960).

The total coverage of *Alopecurus geniculatus* is highest in years with shorter inundations during the growing season. It was negatively influenced by the long inundation in 1980. The same applies for *Trifolium fragiferum* in transect D. *Juncus compressus* on the contrary is favoured by years with a long period of flooding.

Acknowledgement

I am much indebted to Prof.Dr. V.Westhoff and Prof. Dr. M.J.A.Werger for critical remarks, to Drs. O.van Tongeren for his assistance with the computer programs. Sincere thanks are due to ing. H.v.d.Steeg for his advice in the selection of the transect sites, his assistance in measuring the (ground)water levels of the transects D and E and his survey of the altitudinal level of the quadrats. I also wish to thank Drs. A.Kempers for his advice and the graduate biology students W.E. Crusio, T.Duives, T.Pijnenburg, J.van Doorn, R.Schrijnemakers, F.Bloemendaal, R.Schuurkes and J.Thurlings as well as Mr. L.Wiegmans for their assistance in the field.

Appendix.

Table 2. Transect A. Belt transect showing the floristic differentiation of the plant cover in the successive years. a) 1978; b) 1979.

b. Transect A July 1979

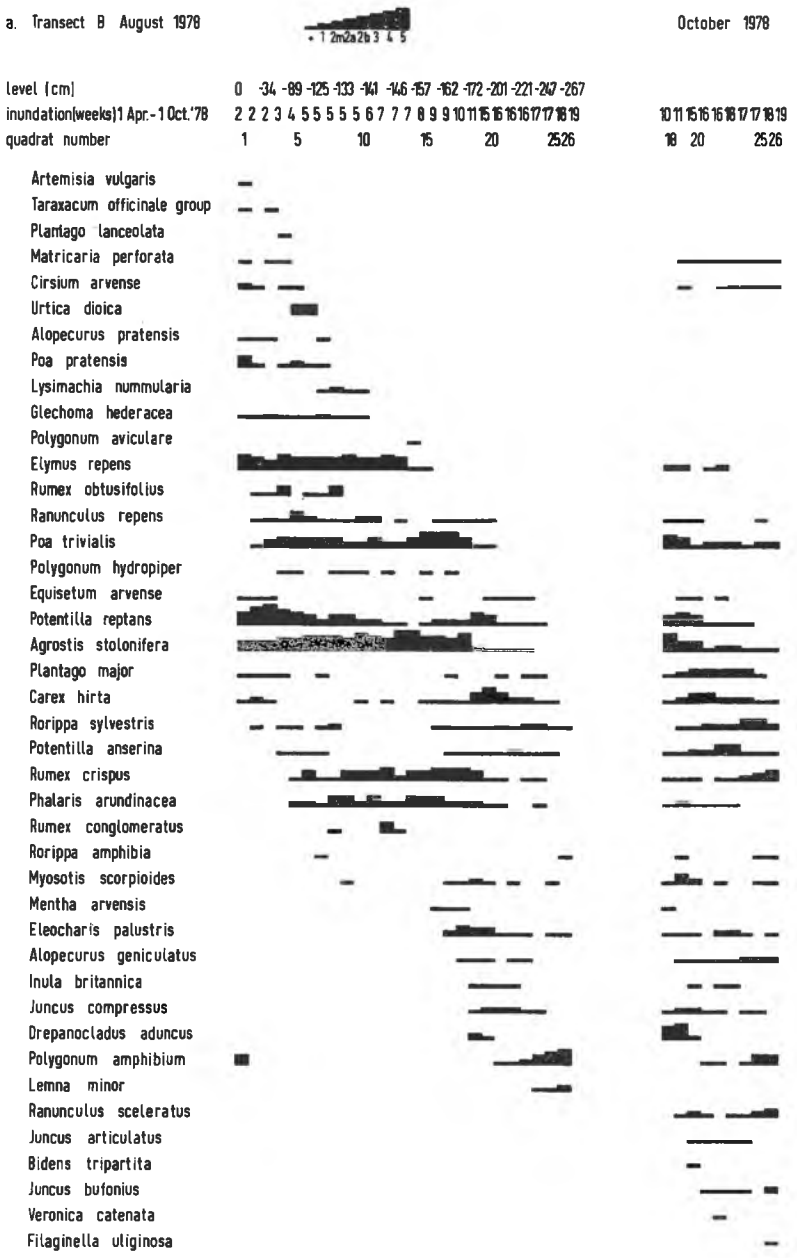
September 1979

inundation(weeks)1 Apr.–1 Oct.'79 3 3 4 4 4 5 5 5 5 5 5 6 7 8 8 9 10 11 11 12 13 13 13 13 13 13 13 14 14 14 14 13 13 13 14 14 14 14

quadrat number 1 5 10 15 20 25 30 25 30

Elymus repens
Glechoma hederacea
Glyceria maxima
Rumex obtusifolius
Poa trivialis
Urtica dioica
Agrostis stolonifera
Ranunculus repens
Rumex crispus
Phalaris arundinacea
Potentilla reptans
Rorippa sylvestris
Mentha arvensis
Rorippa amphibia
Plantago major
Polygonum hydropiper
Myosotis scorpioides
Veronica catenata
Potentilla anserina
Carex acuta
Rumex x acutus
Alopecurus geniculatus
Potentilla supina
Polygonum amphibium
Eleocharis palustris
Polygonum aviculare
Sonchus arvensis
Cirsium vulgare
Poa annua
Chenopodium rubrum
Matricaria perforata
Filaginella uliginosa
Ranunculus sceleratus
Oenanthe aquatica
Limosella aquatica
Bidens tripartita
Stellaria media
Juncus bufonius
Veronica beccabunga
Myosoton aquaticum
Capsella bursa-pastoris
Chenopodium glaucum
Cirsium arvense

Table 3. Belt transect showing the floristic differentiation of the plant cover in transect B in the successive years. a)1978; b)1979; c) 1980; d) 1981.



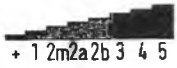
b Transect B July - August 1979

inundation (weeks) 1 Apr.–1 Oct. '79 0 1 1 1 2 2 2 3 3 3 3 3 3 3 5 5 5 5 6 8 10 11 12 13 13 14 14

quadrat number 1 5 10 15 20 25 26

Bellis perennis
Trifolium pratense
Polygonum persicaria
Cerastium fontanum
Polygonum hydropiper
Plantago lanceolata
Poa pratensis
Trifolium repens
Glechoma hederacea
Lysimachia nummularia
Taraxacum officinale group
Rumex conglomeratus
Rumex obtusifolius
Elymus repens
Equisetum arvense
Potentilla reptans
Carex hirta
Ranunculus repens
Cirsium arvense
Plantago major
Agrostis stolonifera
Poa trivialis
Rorippa sylvestris
Calliergonella cuspidata
Phalaris arundinacea
Rumex crispus
Potentilla anserina
Urtica dioica
Myosotis scorpioides
Mentha arvensis
Eleocharis palustris
Alopecurus geniculatus
Juncus articulatus
Atriplex hastata
Polygonum amphibium
Rorippa amphibia
Matricaria perforata
Polygonum aviculare
Juncus bufonius
Ranunculus sceleratus
Limosella aquatica
Riccia cristallina
Filaginella uliginosa
Oenanthe aquatica
Veronica catenata
Potentilla supina
Cirsium vulgare
Chenopodium rubrum

c. Transect B August - September 1980



inundation (weeks) 1 Apr.-1 Oct.'80	6	6	6	7	7	7	7	8	11	12	14	15	16	16	18
quadrat number	13		15					20						25	26
Elymus repens															
Ranunculus repens															
Rumex crispus															
Phalaris arundinacea															
Potentilla reptans															
Agrostis stolonifera															
Rorippa sylvestris															
Carex hirta															
Eleocharis palustris															
Rumex obtusifolius															
Potentilla anserina															
Galium palustre															
Poa trivialis															
Alopecurus geniculatus															
Myosotis scorpioides															
Juncus compressus															
Equisetum arvense															
Rorippa amphibia															
Polygonum hydropiper															
Cirsium arvense															
Plantago major															
Polygonum amphibium															
Mentha aquatica															

d. Transect B September 1981

inundation (weeks) 1 Apr.–10 ct. '81 5 5 5 5 6 8 9 10 11 11 11 13 14 16

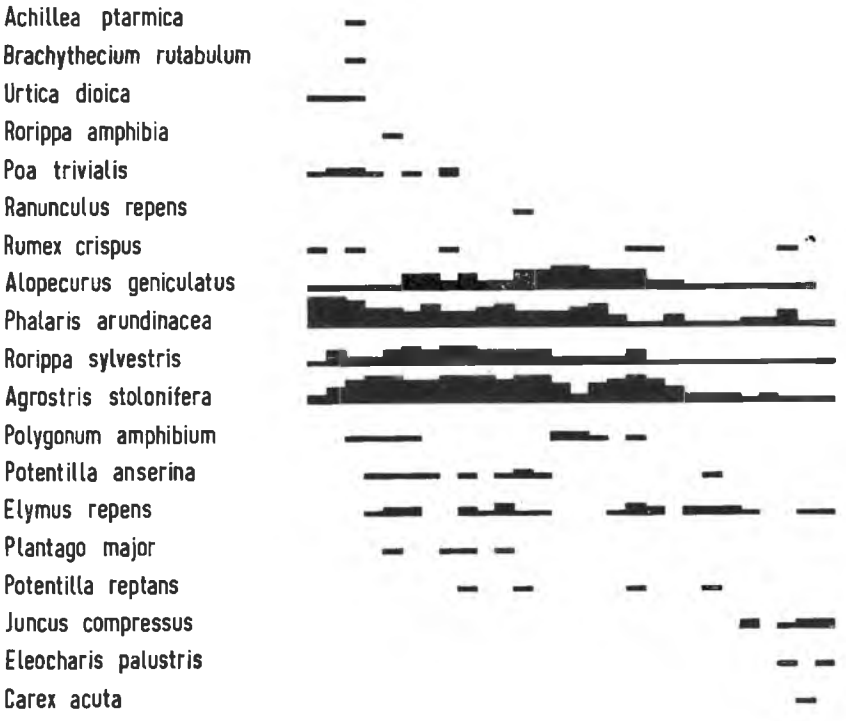
quadrat number 15 20 25 26

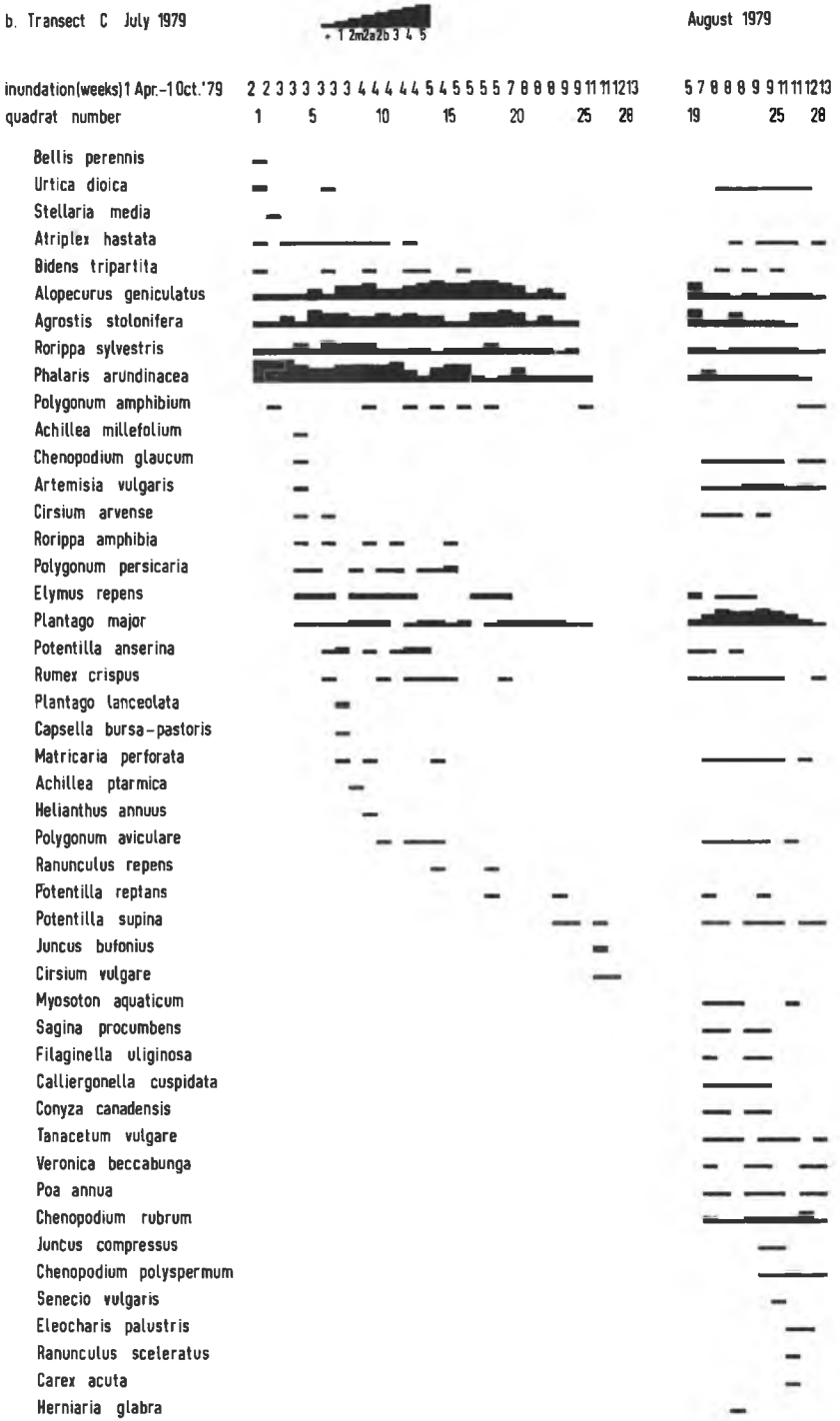
Elymus repens
Mentha arvensis
Rumex obtusifolius
Polygonum mite
Ranunculus repens
Poa trivialis
Bidens tripartita
Potentilla anserina
Phalaris arundinacea
Potentilla reptans
Agrostis stolonifera
Rumex crispus
Carex hirta
Rorippa sylvestris
Polygonum hydropiper
Eleocharis palustris
Galium palustre
Alopecurus geniculatus
Myosotis scorpioides
Rorippa amphibia
Polygonum persicaria
Juncus compressus
Plantago major
Polygonum amphibium
Equisetum arvense
Juncus articulatus
Limosella aquatica
Ranunculus sceleratus
Riccia crystallina
Nymphoides peltata

Table 4. Belt transect showing the floristic differentiation of the plant cover in transect C in the successive years. a) 1978; b) 1979; c) 1980; d) 1981.

a. Transect C August 1978

level (cm)	0	-6	-14	-15	-26	-27	-33	-36	-47	-45	-64	-71	-80	-92	-116
inundation (weeks) 1 Apr.-10ct.'78	5	5	5	5	5	5	5	5	7	7	7	7	8	8	8	10	9	9	11	13	14	15	16	16	16	16	17
quadrat number	1			5				10				15				20					25			28			




b. Transect C July 1979
+ 1 2m2a2b 3 4 5
August 1979
inundation(weeks)1 Apr.–1 Oct.'79
2 2 3 3 3 3 3 3 4 4 4 4 4 5 4 5 5 5 5 7 8 8 8 9 9 9 11 11 12 13
5 7 8 8 8 9 9 11 11 12 13
quadrat number
1
5
10
15
20
25
28
19
25
28
Bellis perennis
Urtica dioica
Stellaria media
Atriplex hastata
Bidens tripartita
Alopecurus geniculatus
Agrostis stolonifera
Rorippa sylvestris
Phalaris arundinacea
Polygonum amphibium
Achillea millefolium
Chenopodium glaucum
Artemisia vulgaris
Cirsium arvense
Rorippa amphibia
Polygonum persicaria
Elymus repens
Plantago major
Potentilla anserina
Rumex crispus
Plantago lanceolata
Capsella bursa-pastoris
Matricaria perforata
Achillea ptarmica
Helianthus annuus
Polygonum aviculare
Ranunculus repens
Potentilla reptans
Potentilla supina
Juncus bufonius
Cirsium vulgare
Myosoton aquaticum
Sagina procumbens
Filaginella uliginosa
Calliergonella cuspidata
Conyza canadensis
Tanacetum vulgare
Veronica beccabunga
Poa annua
Chenopodium rubrum
Juncus compressus
Chenopodium polyspermum
Senecio vulgaris
Eleocharis palustris
Ranunculus sceleratus
Carex acuta
Herniaria glabra

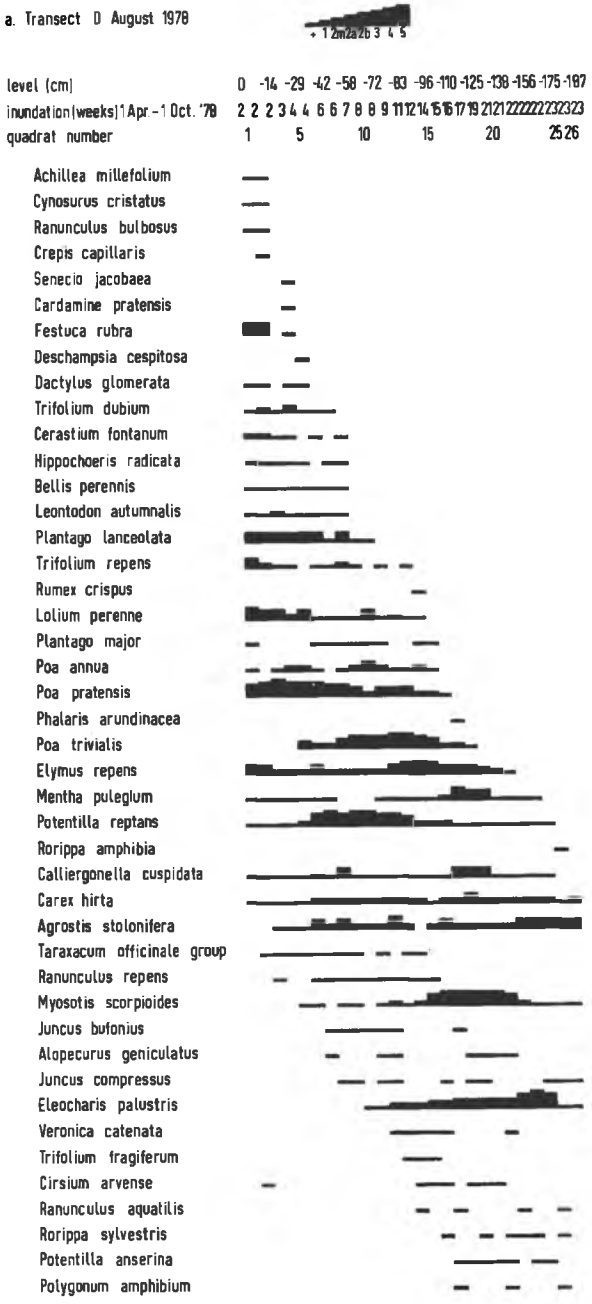
d. Transect C September 1981

inundation(weeks)1 Apr – 1 Oct.'81 2 2 2 2 2 2 2 3 3 3 4 4 4 5 4 5 5 5 5 6 7 8 8 8 9 9 10 10 11

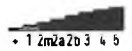
quadrat number 1 5 10 15 20 25 28

Galinsoga ciliata
Veronica beccabunga
Scrophularia auriculata
Rumex obtusifolius
Eupatorium cannabinum
Artemisia vulgaris
Potentilla supina
Stellaria media
Carex hirta
Plantago lanceolata
Poa trivialis
Atriplex hastata
Rorippa amphibia
Taraxacum officinale group
Polygonum persicaria
Urtica dioica
Myosotis scorpioides
Poa pratensis
Agrostis stolonifera
Rumex crispus
Phalaris arundinacea
Rorippa sylvestris
Plantago major
Elymus repens
Alopecurus geniculatus
Potentilla reptans
Potentilla anserina
Chenopodium rubrum
Polygonum aviculare
Matricaria perforata
Ranunculus repens
Polygonum amphibium
Drepanocladus aduncus
Inula britannica
Poa annua
Juncus compressus

Table 5. Belt transect showing the floristic differentiation of the plant cover in transect D in the successive years. a) 1978; b) 1979; c) 1980; d) 1981.



b. Transect D July 1979



inundation (weeks) 1 Apr.–1 Oct. '79 1 2 2 2 2 2 2 3 3 3 3 3 3 3 5 6 6 7 7 12 12 12 13 13 14 15 15 15 15

quadrat number 1 5 10 15 20 25 26

Ranunculus bulbosus
Achillea millefolium
Cerastium fontanum
Festuca rubra
Lysimachia nummularia
Leontodon autumnalis
Trifolium dubium
Dactylis glomerata
Hypochoeris radicata
Bellis perennis
Plantago lanceolata
Taraxacum officinale group
Lolium perenne
Poa annua
Trifolium repens
Poa pratensis
Poa trivialis
Ranunculus repens
Elymus repens
Calliergonella cuspidata
Potentilla reptans
Carex hirta
Agrostis stolonifera
Mentha pulegium
Myosotis scorpioides
Alopecurus geniculatus
Juncus compressus
Eleocharis palustris
Trifolium fragiferum
Rumex crispus
Plantago major
Cirsium arvense
Potentilla anserina
Ranunculus aquatilis
Polygonum amphibium
Rorippa sylvestris

c. Transect D August - September 1980

inundation (weeks) 1 Apr. - 1 Oct. '80 2 2 3 3 3 4 4 4 4 5 5 5 6 6 7 7 8 9 10 11 13 16 18 20 21 23 23

quadrat number 1 5 10 15 20 25 26

Lolium perenne
Leontodon autumnalis
Bellis perennis
Plantago lanceolata
Capsella bursa-pastoris
Taraxacum officinale group
Poa trivialis
Plantago major
Mentha pulegium
Trifolium repens
Ranunculus repens
Juncus articulatus
Elymus repens
Rumex crispus
Polygonum amphibium
Phalaris arundinacea
Potentilla reptans
Carex hirta
Agrostis stolonifera
Myosotis scorpioides
Calliergonella cuspidata
Juncus compressus
Rorippa sylvestris
Eleocharis palustris
Potentilla anserina
Poa annua

d. Transect D September 1981

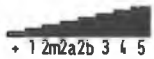
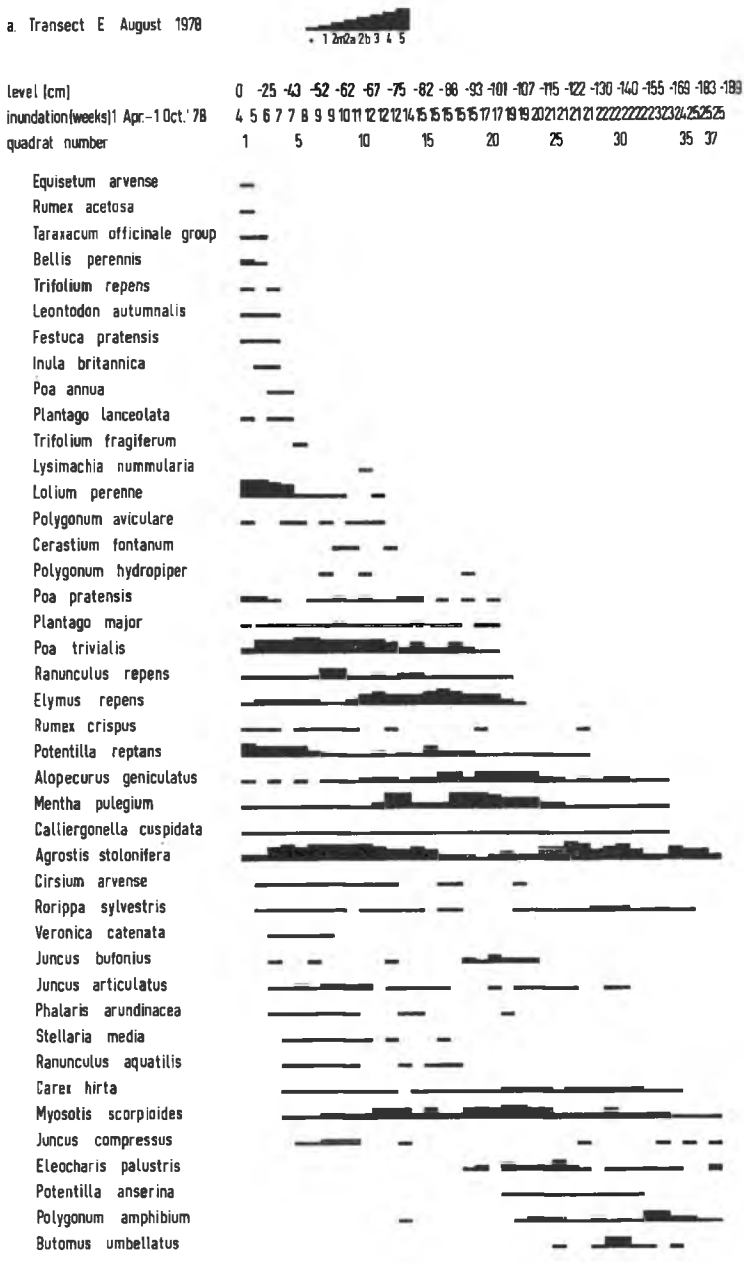
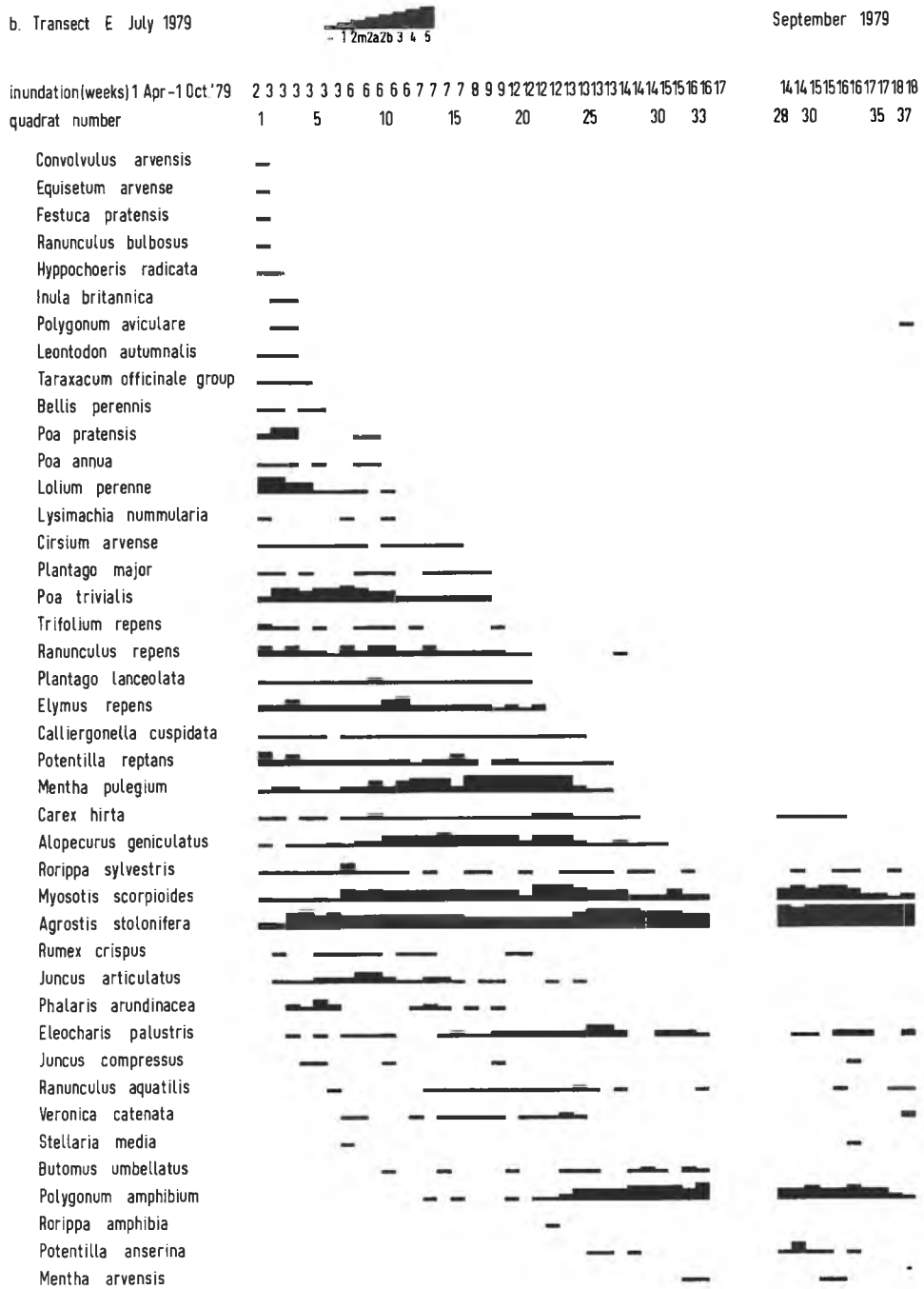


Table 6. Belt transect showing the floristic differentiation of the plant cover in transect E in the successive years. a) 1978; b) 1979; c) 1980; d) 1981.




b. Transect E July 1979
1 2m 2a 2b 3 4 5
September 1979
inundation (weeks) 1 Apr - 1 Oct '79
2 3 3 3 3 3 3 6 6 6 6 6 7 7 7 7 8 9 9 12 12 12 12 13 13 13 13 14 14 14 14 15 15 15 16 16 17
14 14 15 15 16 16 17 17 18 18
quadrat number
1
5
10
15
20
25
30
33
28
30
35
37
Convolvulus arvensis
Equisetum arvense
Festuca pratensis
Ranunculus bulbosus
Hyppochoeris radicata
Inula britannica
Polygonum aviculare
Leontodon autumnalis
Taraxacum officinale group
Bellis perennis
Poa pratensis
Poa annua
Lolium perenne
Lysimachia nummularia
Cirsium arvense
Plantago major
Poa trivialis
Trifolium repens
Ranunculus repens
Plantago lanceolata
Elymus repens
Calliergonella cuspidata
Potentilla reptans
Mentha pulegium
Carex hirta
Alopecurus geniculatus
Rorippa sylvestris
Myosotis scorpioides
Agrostis stolonifera
Rumex crispus
Juncus articulatus
Phalaris arundinacea
Eleocharis palustris
Juncus compressus
Ranunculus aquatilis
Veronica catenata
Stellaria media
Butomus umbellatus
Polygonum amphibium
Rorippa amphibia
Potentilla anserina
Mentha arvensis

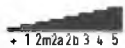
c. Transect E September 1980

inundation (weeks) 1 Apr.–1 Oct.'80 4 4 4 5 5 5 5 6 6 6 6 7 7 7 8 8 8 9 9 9 9 10 11 11 11 11 14 15 16 18 18 20 21 23 25 25 25 26 26

quadrat number 1 5 10 15 20 25 30 35 37

Cirsium arvense
Leontodon autumnalis
Poa trivialis
Calliergonella cuspidata
Elymus repens
Ranunculus repens
Rumex crispus
Potentilla reptans
Rorippa sylvestris
Agrostis stolonifera
Juncus articulatus
Carex hirta
Myosotis scorpioides
Phalaris arundinacea
Eleocharis palustris
Polygonum aviculare
Polygonum amphibium
Juncus compressus
Butomus umbellatus
Lysimachia nummularia
Mentha pulegium
Stellaria media
Alopecurus geniculatus
Drepanocladus aduncus
Potentilla anserina

d. Transect E September 1981



inundation (weeks) 1 Apr.–1 Oct.'81 2 2 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 4 7 7 7 8 9 10 11 12 14 15 16 19 21 22 22 22 32 32 4

quadrat number 1 5 10 15 20 25 30 35 37

Leontodon autumnalis
Plantago lanceolata
Rumex obtusifolius
Lolium perenne
Polygonum aviculare
Inula britannica
Stellaria media
Geranium dissectum
Trifolium fragiferum
Elymus repens
Poa pratensis
Bellis perennis
Rumex crispus
Poa triviałis
Juncus articulatus
Potentilla reptans
Trifolium repens
Ranunculus repens
Alopecurus geniculatus
Taraxacum officinale group
Plantago major
Mentha pulegium
Rorippa sylvestris
Calliergonella cuspidata
Myosotis scorpioides
Agrostis stolonifera
Juncus bufonius
Phalaris arundinacea
Juncus compressus
Cirsium arvense
Bidens tripartita
Carex hirta
Lysimachia nummularia
Centaurium pulchellum
Eleocharis palustris
Polygonum amphibium
Drepanocladus aduncus
Geranium molle
Potentilla anserina
Veronica catenata
Butomus umbellatus
Matricaria perforata

Table 7. Transect A.Comparison of the sum of the transformed cover-abundance values of the species between the years studied. Σc=sum of the transformed cover-abundance values; Δc= difference of cover-abundance.

year	Σc 78	Σc 78	Δc	Σc 78	Σc 79	Δc	Σc 78	Σc 79	Δc
month	Oct.¹	Aug.		Oct.	Sept.		Aug.	July	
quadrats compared	13-30	13-30		25-30	25-30		1-30	1-30	
data compared			Oct.78 Aug.78			Sept.79 Oct. 78			July 79 Aug. 78
Agrostis stolonifera	26	12	+14		4	+4	81	90	+9
Alopecurus geniculatus	84	8	+76	18	17	+1	19	17	-2
Atriplex hastata	2		+2	2		-2			
Bidens tripartita	4		+4	4	8	+4			
Capsella bursa-pastoris					2	+2			
Carduus crispus	2		+2	2		-2			
Carex acuta	19	27	-8	6	10	+4	39	26	-13
Carex hirta	2		+2	2		-2			
Chenopodium glaucum					2	+2			
Chenopodium rubrum	12		+12	10	15	+5			
Cirsium arvense	22		+22	8	4	-4			
Cirsium vulgare				6		-6			
Eleocharis palustris	16	24	-8	6	6		24	25	+1
Elymus repens							9	14	+5
Filaginella uliginosa	10		+10	6	22	+16			
Glechoma hederacea							12	14	+2
Glyceria maxima							7	7	
Juncus bufonius	16		+16	11	16	+5			
Lemna minor	8		+8				8		-8
Limosella aquatica	36		+36	12	17	+5			
Lysimachia nummularia	2		+2						
Matricaria perforata	41		+41	18	33	+15			
Mentha arvensis	9	11	-2		2	+2	13	15	+2
Myosotis scorpioides	16	17	-1	4	4		18	50	+32
Myosoton aquaticum					4	+4			
Oenanthe aquatica	6		+6	4	12	+8			
Phalaris arundinacea	30	32	-2				109	105	-4
Plantago major	89		+89	30	46	+16		31	+31
Poa annua	8		+8	4	8	+4			
Poa trivialis	38	4	+34	2	4	+2	58	52	-6
Polygonum amphibium	23	36	-13	8	20	+12	36	23	-13
Polygonum aviculare	6		+6		6	+6		2	+2
Polygonum hydropiper							17	4	-13
Potentilla anserina	24	30	+4	6	23	+17	26	25	-1
Potentilla reptans	10	4	+6	2		-2	6	8	+2
Potentilla supina					8	+8		16	+16
Ranunculus repens	10		+10		2	+2		24	+24
Ranunculus sceleratus	45		+45	18	15	-3			
Rorippa amphibia	25	6	+19	12	12		10	18	+8
Rorippa sylvestris	62	51	+11	19	17	-2	60	72	+12
Rumex crispus	54	38	+16	23	12	-11	79	36	-43
Rumex obtusifolius	2		+2				48	54	+6
Sonchus arvensis	2		+2		2	+2			
Stellaria media	14		+14	2	6	+4			
Urtica dioica	4		+4				13	23	+10
Veronica beccabunga	6		+6	4	8	+4			
Veronica catenata	11		+11	12	10	-2		2	+2

Table 9. Transect C. For further information see table 7.

year	∑C 78	∑C 79	ΔC	∑C 79	∑C 79	ΔC	∑C 79	∑C 80	ΔC	∑C 80	ΔC	ΔC	∑C 79	∑C 80

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Curriculum vitae

Karel Vaclav Sýkora werd op 27 april 1949 te Djakarta (Indonesië) geboren. In 1967 behaalde hij het einddiploma H.B.S.-A aan het Canisiuscollege te Nijmegen, waar hij zich vervolgens aan de Katholieke Universiteit liet inschrijven als student biologie. Na achtereenvolgens het M.O.- en het kandidaatsexamen biologie behaald te hebben, legde hij op 3 september 1974 het doktoraalexamen biologie af. In het kader van de doktoraalstudie verrichtte hij onderzoek op de volgende vakgebieden: dieroecologie (hoofdvak, o.l.v. Dr.J.J.van Gelder), geobotanie (bijvak, o.l.v. Prof.Dr.V.Westhoff) en genetica (bijvak, o.l.v. Dr.H.F.P.Joosten).

Van 1973 tot 1977 was hij werkzaam als docent biologie aan het Elzendaalcollege te Boxmeer, het Pius X college te Beverwijk en het Instituut voor Hoger Beroepsonderwijs te Eindhoven. In 1976 verbleef hij enige tijd in Pretoria, Zuid-Afrika, waar hij verbonden was aan het Botanical Research Institute.

Dankzij een subsidie van het Beyerinck-Popping Fonds van de Koninklijke Nederlandse Akademie van Wetenschappen kon hij op 1 april 1977 voor een periode van acht maanden verbonden worden aan de afdeling Geobotanie van de Katholieke Universiteit Nijmegen, teneinde een onderzoek in te stellen naar de gevolgen van de extreme droogte van 1976 op de vegetatie van enkele vennen en op de vegetatie van duinvalleien op Terschelling. Per 1 januari 1978 volgde een tijdelijke aanstelling als wetenschappelijk medewerker aan de afdeling Geobotanie. Onder leiding van Prof.Dr.V.Westhoff begon hij een promotieonderzoek naar de syntaxonomie en de synoecologie van het Lolio-Potentillion anserinae TÜxen 1947 in het noordelijk deel van het Atlantisch Domein, waarvan de resultaten in het onderhavige proefschrift zijn weergegeven.

Daarnaast publiceerde hij over verschillende andere phytosociologische onderwerpen waarmee hij tijdens zijn onderzoek in aanraking kwam en die zijn belangstelling trokken.

List of publications

1. C.M.P.Sýkora-Hendriks & K.V.Sýkora (1973):De dijkvegetatie van Zuid-Beveland.Int.rapp.afd.Geobot, in opdracht van het R.I.N. 27 pp, 14 tabellen en kaarten.
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18. H.F.G. van Dijk & K.V.Sýkora (1982): Onderzoek naar de aanwezigheid van kiemkrachtig zaad in de bodem van twee noordlimburgse natuurgebieden. De Levende Natuur 84(5/6):147-152.
19. Sýkora,K.V.(in press): The Lolio-Potentillion anserinae in the northern part of the Atlantic Domain. Acta Botanica Slovaca.
20. Westhoff,V., J.Schaminée & K.V.Sýkora (in press): Aufzeichnungen zur Vegetation der schwedischen Inseln Öland, Gotland und Stora Karlsö. Mitt.Flor.-Soziol.Arb.Gem.

ERRATA

publication I

pag.355,line 2: read: "discussed" for "discused".

publication II

pag.73, line 5 from below: read: "P-citric acid 51-80 mg/100 gr dry sample" for " P-citric acid 51-80".

pag.74,line 18: read: "ecotopic oscillations" for "ecotypic oscillations.

pag.76: At the top of the table should be added: Table 2.Ranunculo-Alopecuretum geniculati.

pag.81: At the top of the table should be added: Table 4. Triglochino-Agrostietum stoloniferae.

pag.83: At the top of the table should be added: Table 5. Agrostio-Trifolietum fragiferi and Ononido-Caricetum distantis.

pag.86: At the top of the table should be added: Table 6. Derivate community of Festuca arundinacea- Lolio-Potentillion .

pag.94, line 10: read: E.H.Franz" for: "H.F.Eldon".

publication III

pag.191,line 6 from below: read: "P-citric acid 80 mg/100 gr dry sample" for " P-citric acid 80".

Bij de presentatie van syntaxonomisch materiaal dient men alle van een gemeenschap gemaakte opnamen in de tabellen weer te geven. Weinig kenmerkende of moeilijk plaatsbare opnamen die in het verleden veelvuldig werden weggezuiverd, blijken vaak tot basis- of derivaatgemeenschappen te behoren.

Zie: dit proefschrift.

II

In tegenstelling tot de mening van den Hartog, is invoering van het begrip "textuur" zoals voorgesteld door Barkman (1979), niet overbodig; noch is het zo, dat dit begrip gedekt wordt door "floristische en faunistische samenstelling".

Zie: den Hartog,C.,Architecture of macrophyte-dominated aquatic communities. In: J.J.Symoens, S.S.Hooper & P.Compère (eds.)Studies on Aquatic Vascular Plants. Bruxelles, pag.224,1982.

III

Voor ontstaan en voortbestaan van het Lolio-Potentillion is het niet van belang dat het zich bevindt tussen twee ruimtelijk contrasterende standplaatstypen. Wel van belang is de aanwezigheid van een "jahreszeitliche ökologische Varianz", met name van de waterstand.

Zie: Westhoff,V.& C.G.van Leeuwen, Ökologische und systematische Beziehungen zwischen natürlicher und anthropogener Vegetation. In:R.Tüxen (ed.) Anthropogene Vegetation. Junk, The Hague, pag.156-172, 1966.

IV

Met de ontwikkeling van numerieke verwerkingsmethoden is de syntaxonomie in een nieuwe fase gekomen. Een revisie van de bestaande plantengemeenschappen met gebruikmaking van deze methoden is dringend gewenst.

V

Het is dringend gewenst dat gebruikers van numerieke methoden bij de verwerking van vegetatietabellen een gedegen kennis van en ervaring met de klassieke verwerkingsmethoden bezitten.

VI

Het Lolio-Potentillion heeft een hoge mate van vervangbaarheid (sensu Londo 1972) en is zeer kenmerkend voor het noordwesteuropese laagland. Desondanks gaat deze gemeenschap als gevolg van de sterk toegenomen anthropogene dynamiek (ontwatering, te intensieve beweiding, bemesting en herbicidengebruik) overal sterk achteruit.

Zie: Londo,G., Over de mate van vervangbaarheid van natuurlijke milieus. Contactbl. v.Oecol. 6(3/4):68-70, 1972.

VII

De opvatting van Duffey:"Poaching invariably is associated with a loss of biological interest" is niet juist. Het ontstaan van gaten in het grasdek biedt een groot aantal soorten kiemingsmogelijkheden.

Zie: Duffey,E.et al.,GRassland Ecology and Wildlife Management.Chapmann & Hall, London, 281 pp, 1974.

VIII

Het is onjuist de iepenval als het begin van akkerbouw en veeteelt te zien.

Zie: Groenman-van Waateringe, W., The early agricultural utilization of the Irish landscape. In: Approaches to landscape archeology in Ireland. F. Hammond en T. Reeves-Smyth. British Archeological Reports. in press.

IX

De voortschrijdende milieuverwoesting maakt van veldbiologen in toenemende mate historici.

X

Ook ten aanzien van het gedrag van een volk ten opzichte van zijn natuur en landschap geldt de ierse wijsheid: "You can't have your loaf and eat it."

In memoriam John Mc Cahill.

XI

Crazy races doen uit het oogpunt van milieuvervuiling, geluidshinder en energieverspilling hun naam eer aan.

XII

Namen van viaducten, benzinestations en eigentijdse onsteden als Gagel, Dassenburcht, het Broek, Lage Heide, Vossenberg, Zwanenveld en Meijhorst zijn een affront voor de natuur die eraan opgeofferd is.

XIII

De gewoonte van politici om de problemen betreffende de emancipatie van de vrouw te rekenen tot de problemen van de emancipatie van minderheden in het algemeen, wekt de indruk dat de kwalificatie "minder" hier niet kwantitatief maar kwalitatief wordt gehanteerd.

XIV

Als rechtvaardiging voor het thuislandenbeleid wordt door Zuidafrikaanse politici o.a. het argument gebruikt, dat de negerbevolking slechts terugverwezen wordt naar het grondgebied waar zij historisch recht op heeft. De uiterste consequentie van deze argumentatie zou betekenen, dat Zuid-Afrika over enige tijd officieel geen blanke staatsburgers meer zal kennen.

Zie: Cosmas Desmond, The discarded People. 1971, pag. 28.

XV

Human knowledge is, at its best, composed of fragments of the truth.

Zie: Christmas Humphrey, Buddhism. Penguin Books, 1969, pag. 90.

Stellingen, behorend bij het proefschrift van K.V. Sýkora, The Lolio-Potentillion anserinae R. Tüxen 1947 in the northern part of the Atlantic Domain.
Nijmegen, 21 April 1983.

SAMENVATTING